ENDOCRINES AND CONSTITUTION IN DOVES AND PIGEONS

OSCAR RIDDLE

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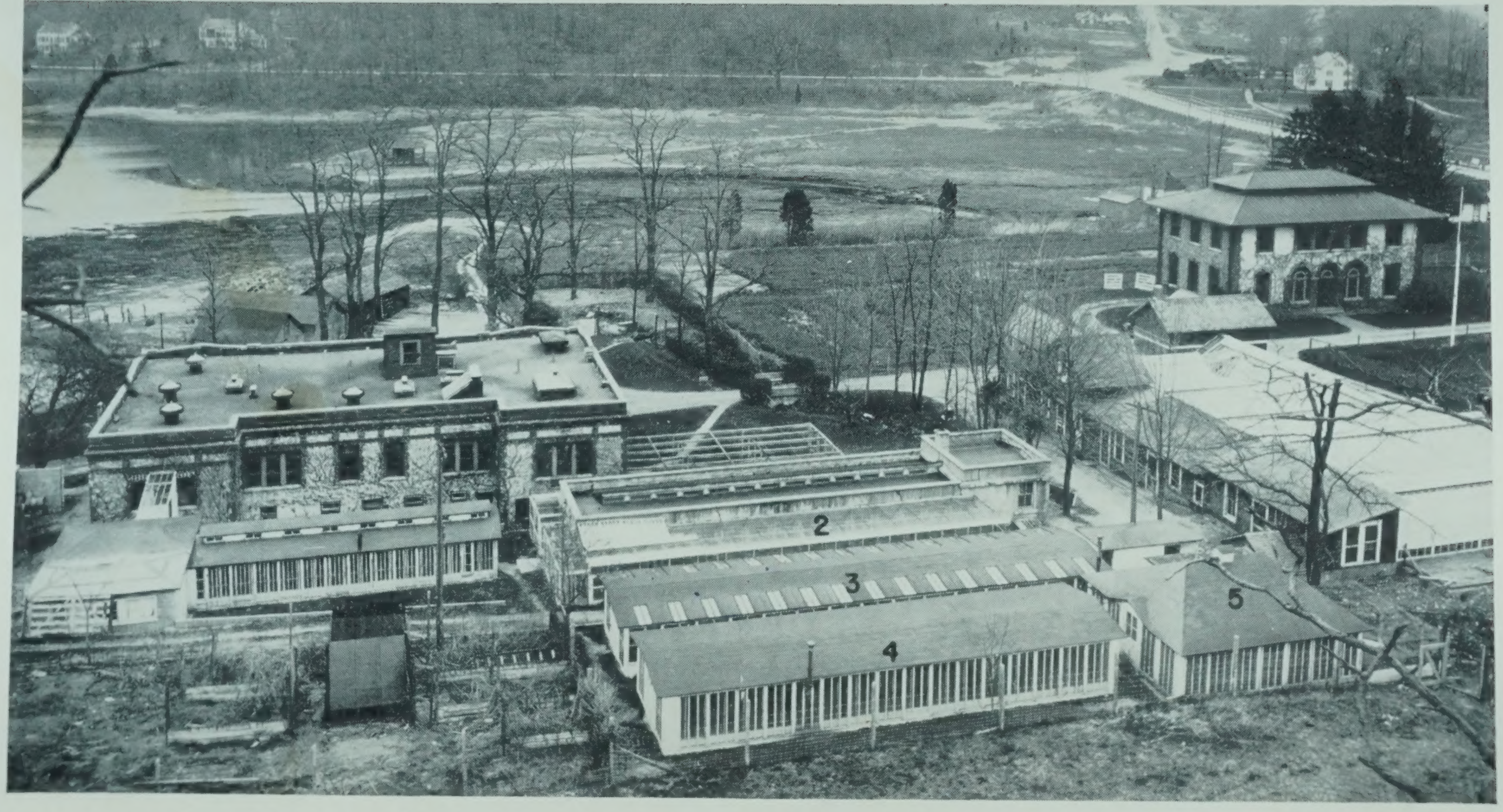

Laboratory and Colony Houses (1 to 5) of the Department of Genetics, Carnegie Institution of Washington, at Cold Spring Harbor, New York

ENDOCRINES AND CONSTITUTION

In Doves and Pigeons

Oscar Riddle

Department of Genetics, Carnegie Institution of Washington

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PREFACE

Darwin and his successors have supplied more precise and comprehensive information concerning the origin and maintenance of new species than we now possess for an understanding of the nature, origin, number, and distribution of those inherited differences which characterize individuals and races of the human species. It is known, however, that abilities and disabilities fill this area of the less known; that the host shares with the infective agent in the onset and progress of disease; and that even social and political policy is or should be conditioned by the diverse innate capacities and incapacities of men. For these and other reasons constitutional differences have become, or are fast becoming, a prime problem of biological research.

In the long and complicated task of recognizing, measuring, and evaluating human constitutional differences—as in the similar and, we believe, better performed task concerning human origin—it seems clear that experimental animals must be expected to supply some basic principles and much indispensable information. A variety of reasons led to the acceptance of doves and pigeons as species especially suitable for one such study. Among those reasons was the fact that the degree of mongrelization present in each of these species is apparently comparable with that in the human population of an American city, and that many facts relating to constitutional factors in these birds are probably applicable to man. Support for that early view has accumulated during the twenty-four years that have elapsed since the present study was started.

The presence of individual differences in a population of doves would be granted, and that point did not require investigation. The primary purpose of the present study was to learn whether certain of the individual differences of doves could be established as racial characteristics, and, if so, to learn whether hormonal differences are associated with one or another of such racial differences. It would seem that facts derivable from a study of this kind should have some definite implications in regard to both individual and racial differences in man. Although success has been attained by many others with regard to such matters as resistance to disease in different races (or strains), no previous study has approximated the purposes of the present effort in a study either of constitution or of the relation of endocrines to constitution.

The center of interest in the present study attaches to the outcome of our attempt to isolate and establish strains or races of ring doves—races showing diverse endocrine-associated traits—from 24 *pairs* of doves (selected from more than 200 pairs) whose reproductive performance and ancestry were fairly well known. In this effort selection sometimes continued for two generations, and inbreeding was practiced throughout. Outcrosses provided many hybrid types, and likewise further tests on the heritability of the traits. The collection of data from parental and hybrid types was continued during 24 years.

During the progress of this study it became evident that we were, in fact, dealing with physiological and structural inequalities of races. The reader will note that we use the word "inequalities," not "differences." Since physical conditions could here be virtually leveled—substantially equalized—and since social, educational, and related influences are wholly improbable in this material, it is concluded that the highly important distinction between "inequality" and "difference" is implicit in the results of this investigation. At the termination of the task of making measurements, it is our duty and privilege to summarize and report upon this variety of tests and observations. The writer is aware of inadequacies in the data submitted for several of the subjects treated in this volume; his satisfaction rests upon a fairly definite answer to the main question and, he hopes, upon partial success in some related fields where certainty often has proved elusive.

Among the individual topics that have been examined in some detail is the role of race, sex, and hybridity in basal heat production. That study is here associated with concurrent studies on weights of thyroids and on still other constitutional factors. This inquiry has provided for populations of doves and pigeons a kind of information which should be obtained also for similar mammalian populations.

It is obvious that the investigation of problems of constitution involves some use of the principles and facts of genetics and of endocrinology. These essential tools are now better developed than in 1921, when this study was planned and started; but readers of this volume are reminded that even now an analysis of some of the present results is hampered or wholly precluded by uncertainties concerning the basic physiology of regulatory mechanisms in higher animals. Very fortunately a large amount of indispensable information has been obtained during the past two decades on the products of the anterior pituitary gland, and on the hormones of other endocrine glands which are regulated largely by the pituitary. If that basic information had not thus become available, large segments of the present data could not now be discussed in terms of endocrine constitutional factors.

Cold Spring Harbor, New York
July 1945

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ACKNOWLEDGMENTS

Much of the labor involved in obtaining the present data, and in summarizing, analyzing, and presenting them, has been generously shared by many others. The following assistants, each during at least one year, shared in the daily inspections of the breeding colonies and in the weighing and measuring of organs: Mr. John R. Spannuth, Mr. Walter S. Fisher, Mr. Paul Frey, Mr. Warren H. Reinhart, Miss Frances H. Burns, Miss Florence Flemion, Miss Marguerite Comunale, Miss Irene Polhemus, Miss Pela Fay Braucher, Mr. Donald R. Charles, Mr. Joseph I. Thaler, Mr. George E. Cauthen, Mr. Simon W. Dykshorn, Mr. Ernest L. Lahr, Dr. James P. Schooley, Dr. Richard A. Miller, Dr. Mychyle W. Johnson, Mr. Louis R. Stillwell, Jr., Mr. Leonard H. Elwell, Mr. Dale Hennon, Dr. H. H. Dunham, Mr. Graham Erdwurm, Dr. H. H. Marvin, and Miss Vita M. Rauch. To each member of this group, and also to Dr. Robert W. Bates, the writer is much indebted.

During nearly seventeen years Mrs. Guinevere Christman Smith has rendered special assistance in connection with the measurements of heat production. In this same work Miss Theodora Nussmann gave assistance during one year. At the beginning of these studies on heat production we had the able collaboration of Dr. F. G. Benedict, then Director of the Carnegie Institution of Washington's Nutrition Laboratory, Boston, Massachusetts. Parts of the apparatus used in our measurements of heat production were devised and built under his supervision, and to him we are greatly indebted.

From the beginning Miss Mary Holmes has rendered invaluable assistance with the records, both of the breeding colony and of the laboratory data. To her, moreover, we owe much connected with the typing and checking of this manuscript. For recent able assistance with the literature and manuscripts dealing with heat production, our sincere thanks are due to Professor Hoyt S. Hopkins, of New York University. In the task of analyzing and summarizing a formidable amount of breeding data, Dr. Willard F. Hollander has rendered an important service. He also contributed much to the statistical treatment of the data, and otherwise aided in the preparation and reading of the manuscript.

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Part I

1

INTRODUCTION

Darwin[1] studied many of the domestic breeds of pigeons intensively. After noting instances of their remarkable differences in body size and skull formation he made the following remarks:

> In the skeletons of the several breeds, the development of the bones of the face, in length and breadth and curvature, differs enormously. The shape, as well as the breadth and length of the ramus of the lower jaw, varies in a highly remarkable manner. The caudal and sacral vertebrae vary in number; as does the number of the ribs, together with their relative breadth and the presence of processes. . . . The proportional width of the gape of mouth, . . . the size of the crop and of the upper part of the esophagus; the development and abortion of the oil-gland; . . . the relative length of the leg and foot, . . . are all points of structure which are variable. The period at which the perfect plumage is acquired varies, as does the state of the down with which the nestling birds are clothed when hatched. The shape and size of the eggs vary. The manner of flight, and in some breeds the voice and disposition, differ remarkably. Lastly, in certain breeds, the males and females have come to differ in a slight degree from each other.
>
> Altogether at least a score of pigeons might be chosen, which, if shown to an ornithologist, and he were told that they were wild birds, would certainly be ranked by him as well-defined species. And [some types would not be put] in the same genus.

It should be remembered, however, that the more than 200 races of domestic pigeons may (or may not) have been derived from hybrid ancestors, carrying the blood of two or more wild species. Though authorities disagree on that point, it is generally recognized that pigeons have been associated with man for a period which probably much antedates the recorded history of man; and that, for some thousands of years, selective breeding of pigeons has been actively practiced by many human populations.

No previous study has attempted to establish races of the blond ring dove (*Streptopelia risoria*), nor have the structural, physiological, or temperamental differences of individuals of this species been seriously examined. It will be noted below that blood of another genus (*Turtur*), or of one or another of two species closely related to *risoria*, entered into some of the "races" or types considered in this study. The nomenclature used here in referring to those species is that adopted by Whitman,[2] who, during several years, observed and hybridized the various species of this group. Indeed, birds bred or purchased by Dr. Whitman were the ancestors of the birds later selected to found most of the dove races with which this volume is chiefly concerned.

---

[1] Darwin, Charles, The origin of species (6th London ed., New York).

[2] Whitman, C. O., Inheritance, fertility, and the dominance of sex and color in hybrids of wild species of pigeons. Vol. 2 of Posthumous works (Carnegie Inst. Wash. Pub. 257, 1919).

At this point it would perhaps be of interest to list the characteristics which have been segregated into a series of races (or types) derived from pure *St. risoria* ancestors (see below). Such a list would in no way approach or imitate the diversity of size and structure represented in familiar breeds of domestic pigeons; but the extent to which a series of significant functional levels have been segregated in dove races in the present study would more closely approach the comparable accomplishment in pigeons. This chapter, however, is not concerned with results of investigation; its purpose is to give an account of the living material, the procedures, and the methods utilized in the segregation and examination of certain constitutional factors in doves and pigeons.

DOVE RACES

Ancestry of Doves Chosen for the Establishment of Dove Races

The origin of all the *doves* used in this study traces to 14 birds (see pedigree chart, fig. 1), except for the races *B*, *W*, *K*, and *G*. The exceptional pairs of birds which served as the foundation for the 4 last-named races were all undoubtedly blond ring doves (*St. risoria*) unmixed with any other species, and they were obtained (Boston; Knoxville, Tenn.; Long Island, N. Y.) after the other dove races had been established; races *K* and *G* were used only during the seven terminal years of the study. Two of the "original" 14 birds were captured individuals of wild species: one, a female Oriental turtle dove (*Turtur orientalis*); the other, a male Japanese ring dove (*St. douraca*). A third bird (ADR) was an F_1 hybrid obtained by Dr. C. O. Whitman from a cross of a female Japanese ring dove (*St. douraca*) with a male domestic ring dove of mixed origin, the father of this male being a blond ring dove (*St. risoria*) and its mother a white ring dove (*St. alba*). Most authorities do not accord specific rank to *alba;* and it is practically certain that most of the "white" doves obtainable from dealers, like the "whites" frequently obtained from blond rings in the present study, are merely a color variety of *St. risoria*. Except the male of pair "D," the remaining birds were all domestic ring doves (*St. risoria*)—pairs (or trios) obtained from different sources and characterized in figure 1 by the letters A, D, E, J, and L. "A" was a pair of ring doves, of white color, reared by Dr. Whitman. "L" was a pair purchased in 1912 from a Chicago dealer. "J" was a trio purchased in 1914 but possibly also tracing to Whitman's colony. "E" was a trio purchased in 1914 from a New York dealer. Pair "D" consisted of the male *douraca-risoria-alba* (ADR) mentioned above and a female purchased in Chicago in 1912.

The Selection and Establishment of Races of Doves

To one extent or another the descendants of the "original" 14 birds were mated *inter se* for a varying number of generations. Later, in 1921 to 1923, 24 *matings* whose own reproductive records (or ancestry) pointed to one or another inter-

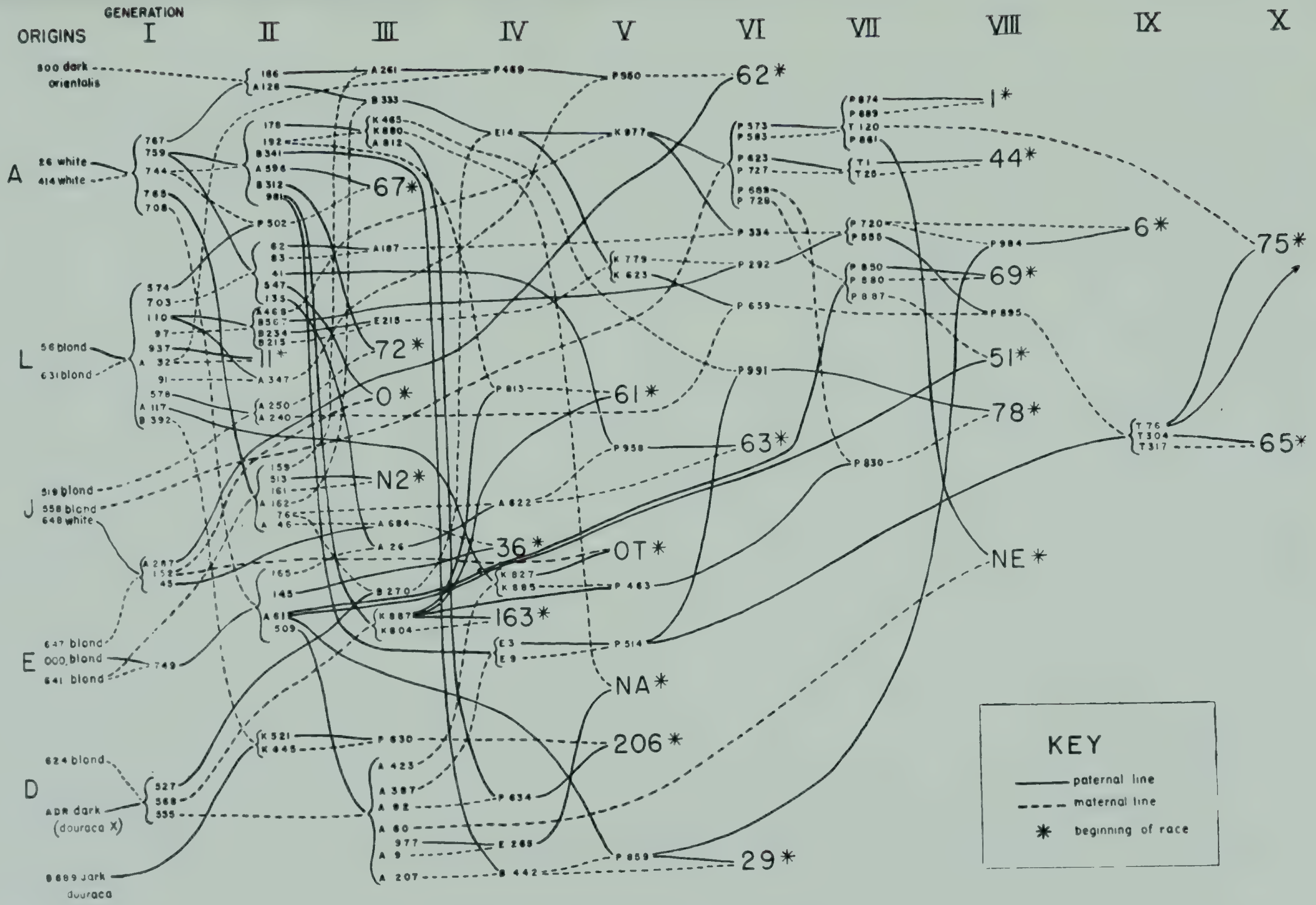

FIG. 1. Network analysis of origin and relationships of dove races

esting result were isolated genetically and no further mixing was permitted; these 24 matings were selected from somewhat more than 200 mated pairs. These isolated pairs, indicated by asterisks (*) on the pedigree chart (fig. 1), usually already had two living generations of offspring; and these offspring had been derived from two or more matings of sibs. When sufficient numbers of F_2 individuals had been obtained from two or more different pairs of F_1 parents, a further selection intervened in some, though not all, cases. At the time this further selection was carried out, the organ weights of the P_1 and F_1 generations (also of many other unselected birds in the colony) were available; and, as noted, some or several aspects of reproductive performance in the family were known. With these data at hand it was possible to select the particular F_2 families which seemed most likely to carry factors for low or high thyroid weight, or for unusually long or short intestines; and only the offspring from these particular F_2 families were permitted either to live or to breed further. In each instance this selection sought to perpetuate the extreme of the condition (of the thyroid or intestine) that was more or less generally evident in the family; and only one of these organs (thyroid or intestine) was made the basis for selection in any one race.

At this point it is convenient to drop the word "matings" and to speak of races. Races 62, *11*, 65,[3] and 72 were selected for large thyroid size; races 75, 29, 36, and *61* for small thyroid size. Races *N2*, *44*, *6*, and *63c* (lost immediately and omitted from pedigree chart) were selected for unusual maximal length of the intestine; races *163*, *O*, *NA*, and 78 for minimal length of the intestine. Eight races (*206*, *1*, *51*, *NE*, *OT*, *63*, *67*, *69*) were essentially normal in most observable aspects of reproduction, and the earliest observations made on P_1 or F_1 of most of them indicated less chance than in other races to obtain unusual thyroid size or intestinal length. For these 8 races selection extended only to the pair of birds isolated for the foundation of the race. The parents chosen to start race *51* produced many defective offspring (cross-bill and a heritable head tremor, myoclonus).

Guide lines on the pedigree chart lead from the names (or numbers) of the races to the particular pair of birds selected to provide the beginning of the 23 races. Data obtained from a few of the least numerous and most closely related of these groups have been combined in all the tables and graphs of part I. This procedure was required by the paucity of data for healthy birds of some races, and it is warranted since only related groups were united and no marked difference in either intestinal length or thyroid weight was observable in data obtained from the groups that were united. Thus, race *69* is grouped with *51*; *1* with *44*; *O* with *OT*; and (except for thyroid weights) *163* and *61* with race *29*. By this procedure the 23 pedigreed races are reduced, for the study of most organ weights, to 18. Races *11* and *206* were lost early, but their hybrids were bred for several generations. This study therefore is concerned primarily with 18 races of doves, each of which was derived from 2 to several of 14 "original" birds, plus 4 additional inbred groups—*B*, *W*, *K*, and *G*—derived from 4 pairs of doves which had a different and probably quite distinct lineage.

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[3] In an earlier publication (Riddle, O., Amer. Naturalist, 1929, vol. 63, p. 385) this race was referred to as race *50*.

Classification of Races According to the Species Represented in Them

The relative contribution, or lack of contribution, of any one of the 14 "original" birds to one or more of the 18 (or 23) races is too difficult in most cases to describe by text. However, by dividing the 14 "original" birds into seven groups, based mainly on their diversity and lack of close relationship, it is possible to indicate in graphic form (fig. 2) the theoretical contribution of any "original" pair to the 18 (or 23) races studied. From the sectorial graphs of the various races it is possible also to estimate roughly the theoretical similarity or disparity of the genetic make-up of any two races.[4] Thus, *N2* and *11* have no original stock in common, whereas *NA* and *29* have very similar composition. More important, however, is the fact that these sectorial graphs indicate the extent to which various *species* of doves were represented in the ancestry of each race. From this point of view these races fall into four groups: Group I, mostly *Streptopelia risoria*, but a slight admixture of *Turtur orientalis;* represented by race *62*. Group II, both of the above-named species (or genera) plus some *St. douraca;* represented by races *NE*, *1*, *51*, *44*, *78*, *75*, *69*, and *65*. Group III, *St. risoria* and *douraca* only; represented by races *NA*, *OT*, *29*, *61*, *206*, *163*, and *6*. Group IV, races containing only *St. risoria;*[5] represented by races *N2*, *72*, *63*, *11*, *36*, *O*, and *67* (also *W*, *K*, *B*, and *G*, started later).

The diversity represented in the above groups seems fairly comparable—particularly if races containing *Turtur* be left out of account—with the diversity found among existing races of men.

Turtur orientalis is usually considered generically distinct from *St. risoria*, though one authority classes both species within the genus *Streptopelia*. It is notable that 9 of the 23 pedigreed races contained small amounts (1/32 to 1/128) of *Turtur* blood. *Douraca* usually has been regarded as specifically distinct from *risoria*, but one observer (Peters) who apparently saw no live specimens classified it as only a variety of *risoria*. A total of 15 pedigreed races contained varying admixtures (1/4 to 1/64) of *douraca* blood; in some of these cases both *orientalis* and *douraca* blood was admixed with *risoria*. Seven pedigreed races, and 4 additional inbred strains, were *risoria* only. Within this frame of mongrel or hybrid origin, or lack of it, the two members of the various pairs which founded the races were of many degrees of consanguinity. In a few cases the two parents were, in effect, wholly unrelated (*206* and *O*); in many cases they were brother and sister (*11*, *N2*, *163*, *1*, *44*, *65*, and *69*), and in some of these same cases the parents of the pair were also sibs (*1*, *44*); in still other cases the two birds used to initiate races were mother and son or father and daughter (*6*, *29*, *51*, and *61*); in addition, many parents and grandparents were further related to one extent or another.

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[4] This assumes that multiple-factor inheritance governs the variation under consideration.

[5] This assumes that white color, often present, does not warrant the view that a white species (*St. alba*) was its source.

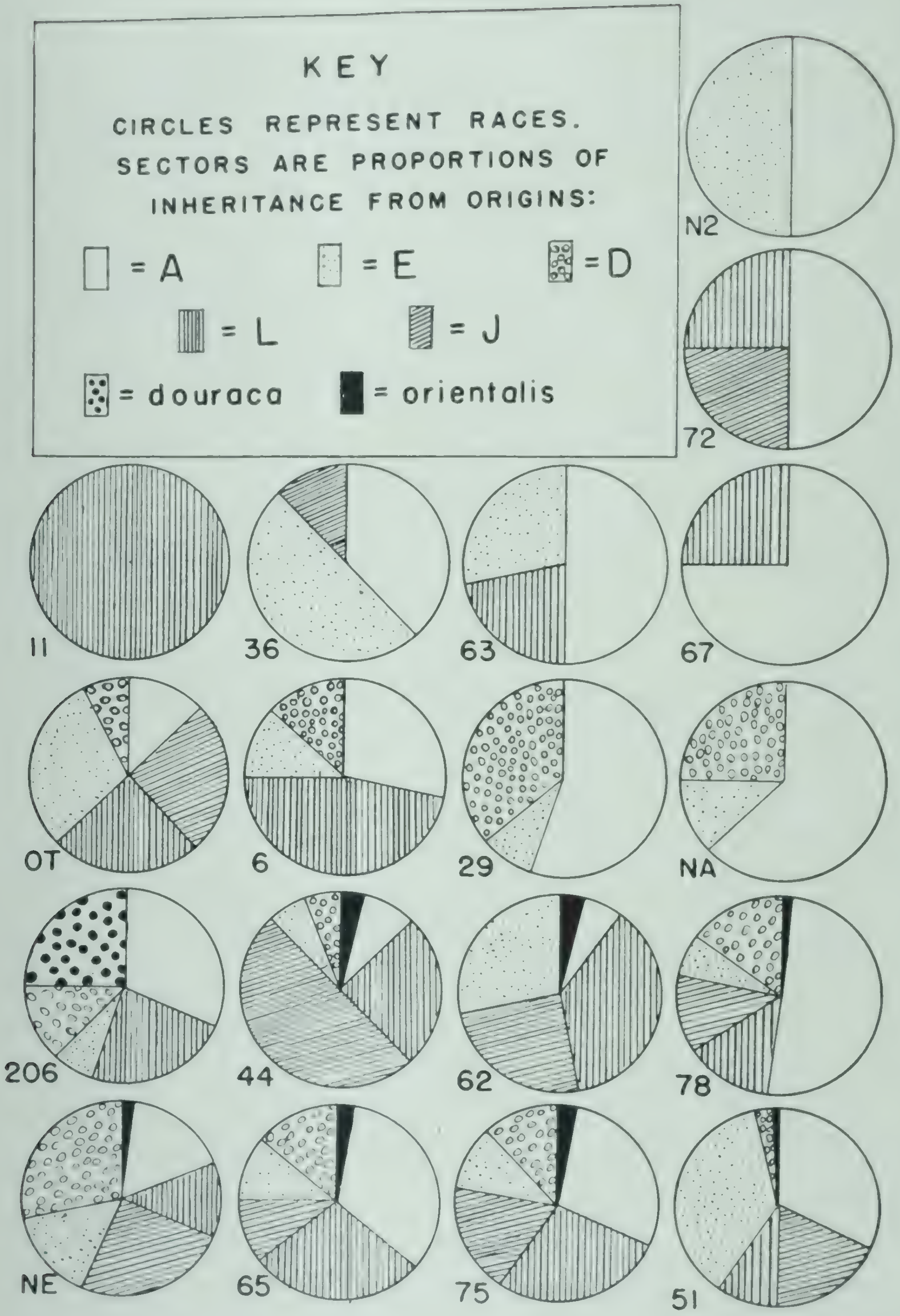


Fig. 2. Sectorial graphs showing the extent to which certain ancestral types were represented in 18 dove races. It is notable that one-fourth of the area of all *D* sectors represents blood of *Streptopelia douraca.*

Photographs of some of the particular birds represented in the ancestry of one or of several races are shown in plate 1. Other individuals which are representative of races or of hybrids at the conclusion of the study are shown in plate 2. A representative of race *62* and one of *N2* × *44* hybrids are shown in plate 3.

Leaving out of account those races which carried the blood of two (or three) species, it can be said that several of these dove races are roughly analogous to small isolated populations in nature, such as have been treated by Dobzhansky[6] and others. That is, unlike homozygous strains produced by protracted intense inbreeding, these races were more or less heterozygous; they probably differed chiefly in gene frequencies. It is therefore to be expected that some overlapping variation will be found even in characters most distinctive for the races, and even when environmental influences are ignored.

Statement on Later History of the Several Races

A condensed statement on certain features of the history of the several races, following their establishment, seems useful at this point. In some degree these summaries indicate the difficulty of maintaining a race of doves when intense inbreeding (brother-sister matings) is practiced. It was noted above that data from 5 races (which produced very few healthy descendants) have been joined to data obtained from another closely related race.

Group I

Race *62*. Eleven generations; moderate inbreeding. A few white offspring.

Group II

Race *NE*. Five (small) generations; mainly by sib matings. Mostly blond offspring.

Race *51*. Twelve generations, and still exists. Intense inbreeding for a few generations, then relaxed. A few white offspring in early generations; none later. A head tremor, apparently "myoclonus complexus," was continuously present in some individuals of this race. The mode of inheritance of myoclonus was not fully analyzed, but it apparently behaved as a simple recessive to normal.

Race *44*. Three generations; mainly by sib matings. Blonds only.

Race *78*. Six generations; by sib matings. A few white offspring, others blond.

Race *1*. Three generations; by sib matings. Blonds only.

Race *75*. Fourteen (or more) generations, and still exists. Inbreeding moderate, and race derived largely from ♂T76. Blonds only.

Race *65*. Fifteen generations; inbreeding intense at first but not later. Blonds only.

Group III

Race *NA*. Thirteen generations; moderate to intense inbreeding, but inconsistent. Dark, blond, and white offspring.

Race *29*. Five generations; fairly intense inbreeding. Some white offspring.

[6] Dobzhansky, Th., Genetics and the origin of species (2d ed., Columbia Univ. Press, New York, 1941).

PLATE 1

Birds actually represented in the ancestry of various dove races. Photographed (mostly) June 1916.

Above. Group "L" of pedigree chart (♂ 56 and ♀ 631), pure *Streptopelia risoria.* The two young shown in the nest are grandchildren, whose parents were brother and sister. One or both of these young contributed to races *6, 1, 44,* and *65.*

Center. F_2 offspring of birds ADR and 624 (group "D" of pedigree chart) containing the two species *St. risoria* and *douraca;* these offspring were of three colors, white, dark, and blond. The two species, *risoria* and *douraca,* were represented in races *163, 206, 61, OT, 6, NE, NA,* and *78.*

Below. The small blond bird at right, ♀ A60, is the mother of race *NE.* The much larger mate is typical of hybrids containing one-fourth *Turtur orientalis* and three-fourth *St. risoria.* Smaller amounts of *orientalis* blood were present in races *NE, 1, 62, 51, 44, 78, 75, 69,* and *65.*

Plate I

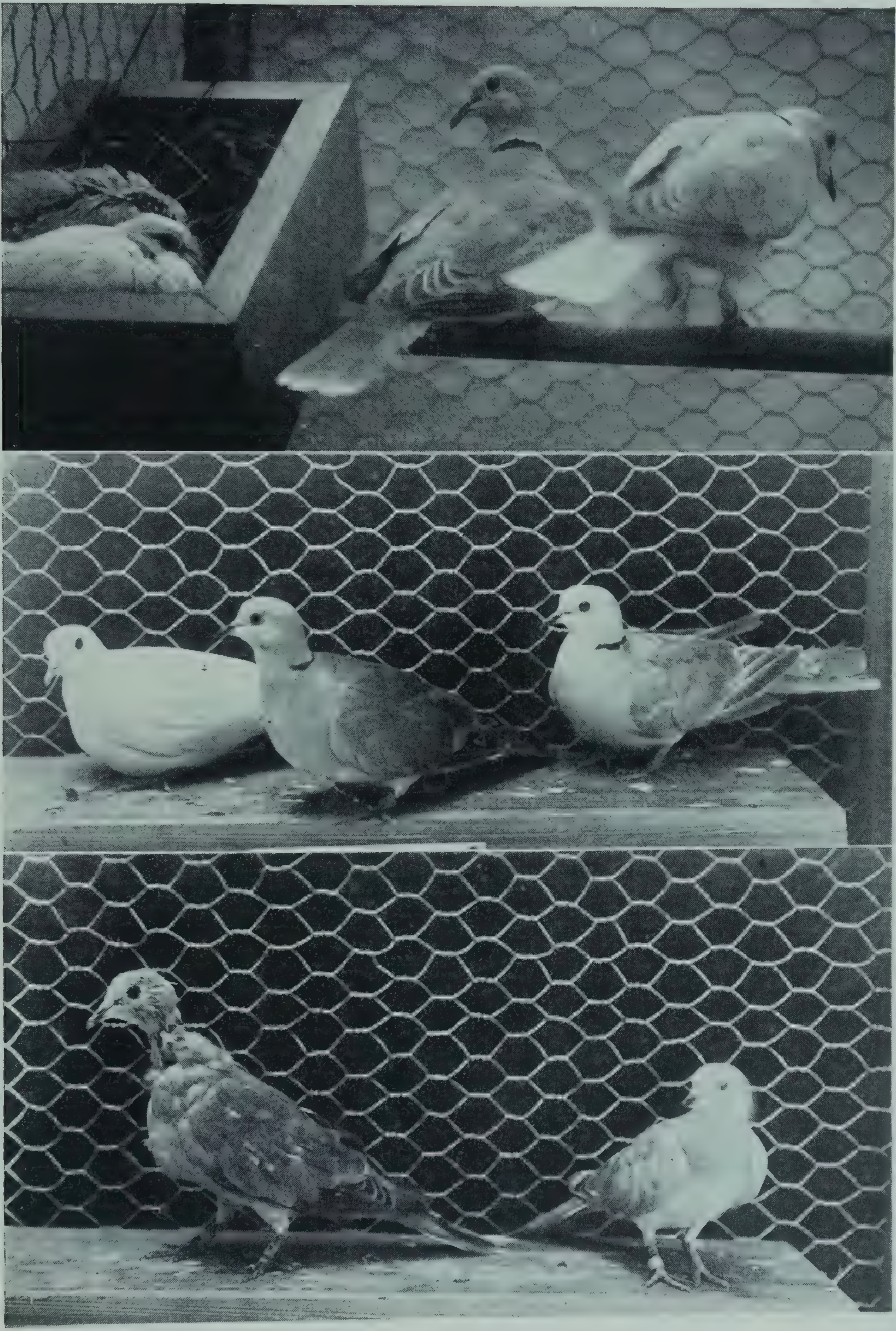


PLATE 2

Representatives of dove races and hybrids at the conclusion of the present study. Photographed February 1945.

Above. Race *75,* smallest thyroids (at left), blond female. Hybrid from races *N2* and *62* (at right), blond male.

Center. Race *51,* normal male of race carrying myoclonus (at left), blond. Hybrid female of races *O* and *72* (middle), white. Race *72,* very late sexual maturity (at right), blond.

Below. Hybrid male from races *51* and *63* (at left), blond. Hybrid male from races 72 and *NA* (at right), dark, but females of three colors obtainable.

PLATE 2

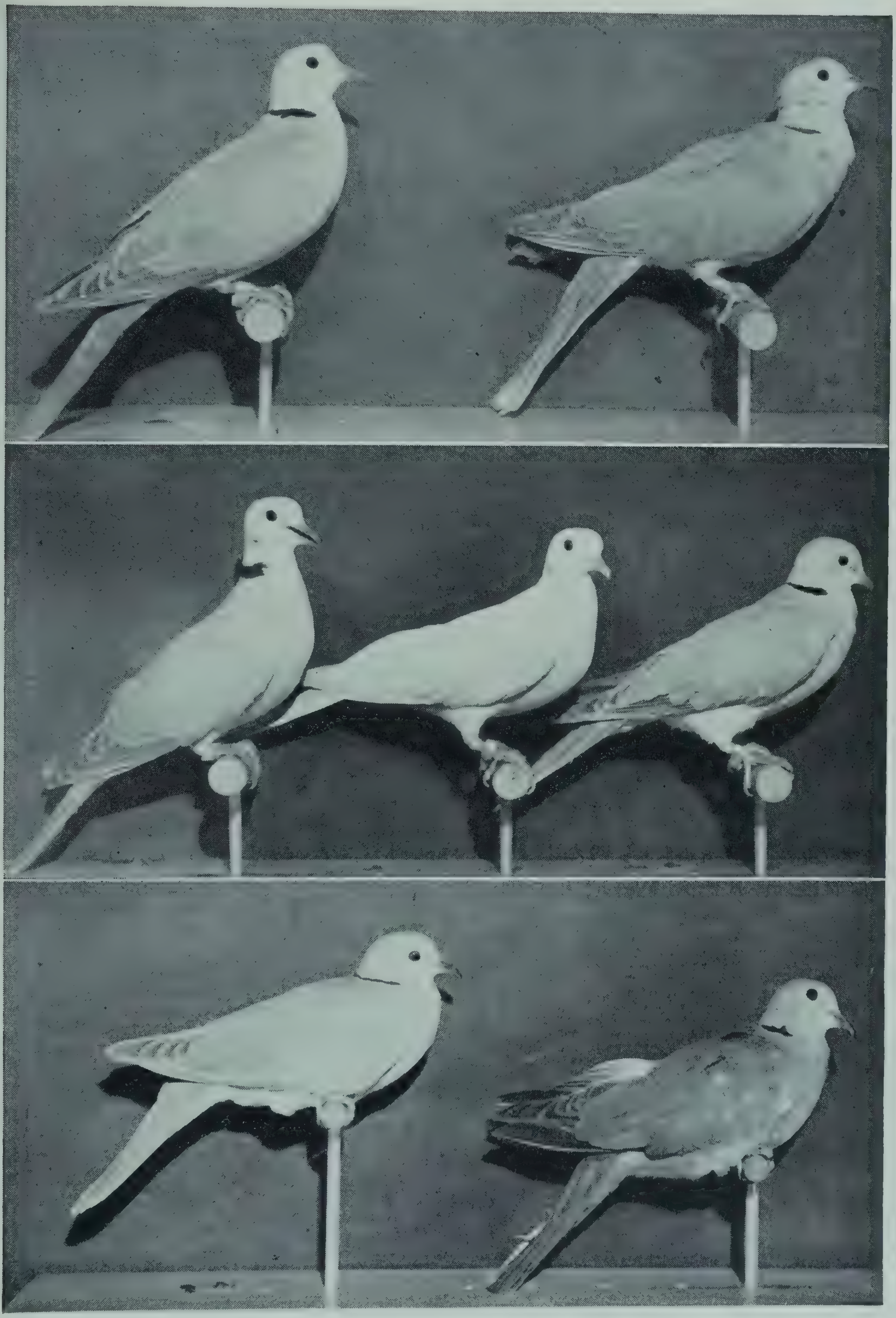


PLATE 3

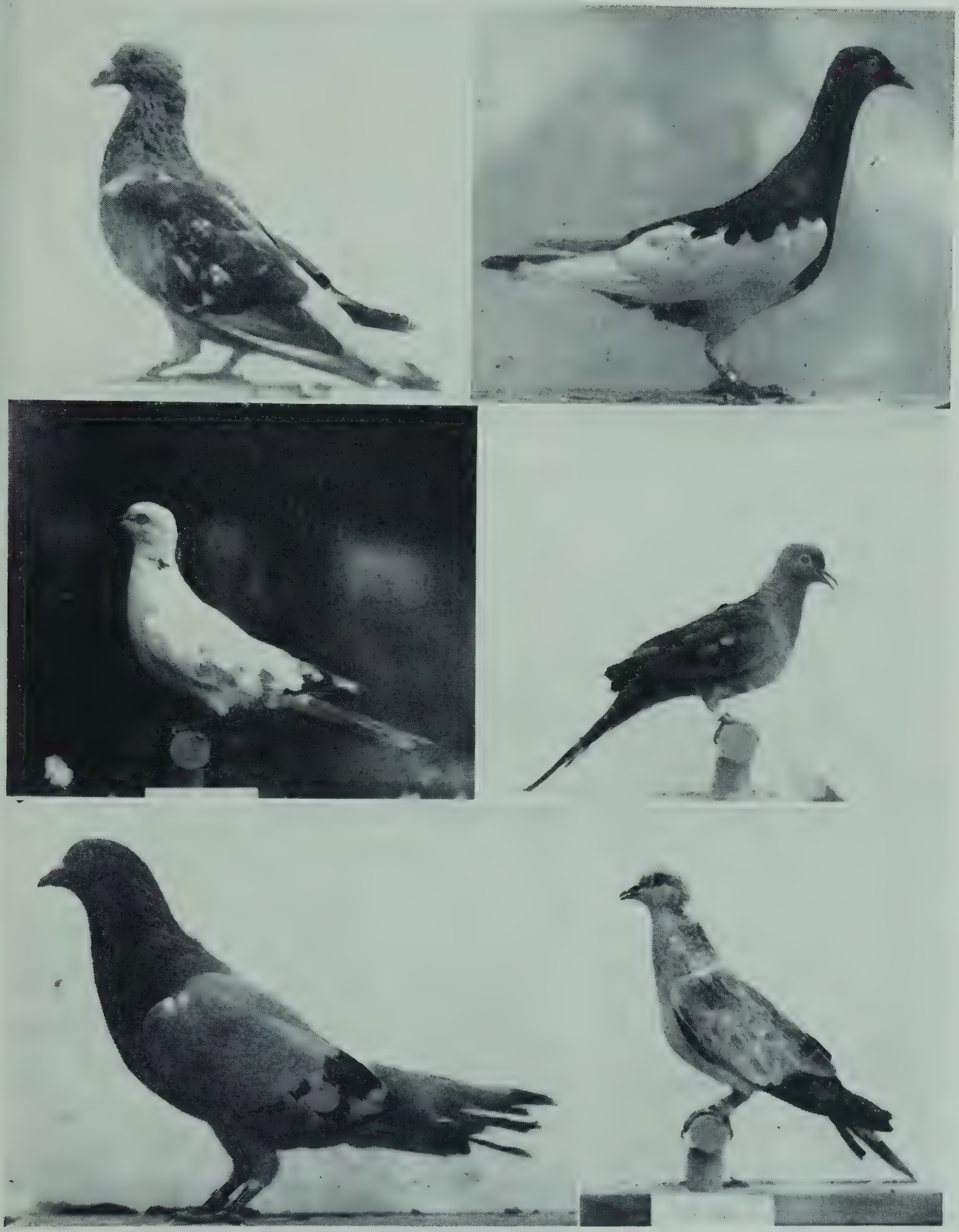
Six types currently studied and photographed (to scale) during the summer of 1930.

Above. Homer male (at left). Magpie female (at right).

Center. A "mottled," white and brown, dove hybrid (♂ H78) from races *N2* and *44* (at left); these hybrids had extremely long intestines and a high metabolic rate. Race *62*, female (at right); this race had very large thyroids and a very low metabolic rate.

Below. Runt female (at left). Hybrid male from a cross of a pigeon and a ring dove (at right).

PLATE 3



Race *206*. Two generations; by sib matings. Some white offspring.

Race *6*. Nine generations; moderate inbreeding. Blonds only.

Race *OT*. Nine generations; intense to moderate inbreeding, but inconsistent. Offspring mostly white.

Group IV

Race *N2*. Nine generations; moderate inbreeding. Mostly blond, but some white offspring.

Race *72*. Sixteen generations, and still exists. Inbreeding moderate to slight, and inconsistent. Approximately one-third of offspring white, others blond.

Race *11*. Three generations; intense to moderate inbreeding. Blonds only.

Race *67*. Nine generations; rather intense inbreeding. Mostly blond.

Race *36*. Five generations; sib matings only, and then became extinct. A few white offspring.

Race *63*. Eleven generations; intense to moderate inbreeding. Very few white offspring.

Race *W*. Four generations; moderate to intense inbreeding. Blonds only.

Race *B*. Eight generations; intense to moderate inbreeding. Blonds only.

Race *K*. Three generations; partly intense inbreeding (a backcross of an F_1 female to the original male was included). Blonds only.

Race *G*. Five generations; little inbreeding. Blonds only.

Concerning Hybrids Obtained from Dove Races

Most of the races described above were crossed with at least one other race and the resulting hybrids propagated over a few to several generations. Seven races were thus crossed with 3 to 9 other races. From certain crosses a significant number of generations and offspring was not obtained, for one or another of the following reasons: The concurrent breeding of so many types, within limited space, greatly restricted the number of breeding pairs of each type; disease played a part; other studies pursued simultaneously required a continuous supply—sometimes too many—of the young doves. Again, close inbreeding in doves, under the conditions imposed by us, was unfavorable to their maintenance and propagation. Those crosses which yielded healthy offspring in numbers sufficiently large to warrant analysis are listed in table 1.

In making these crosses it was assumed that the individual birds used were really representative of their respective races. When F_1 were obtained from three or more different matings this assumption was perhaps justified.

Pigeon Races

Most of the races of pigeons used in this study are in some respects not comparable with the dove races used, and objectives were only partly the same in studies conducted on the two groups. In part, pigeons were well defined and quite divergent types which fanciers had formed by selection decades or centuries ago. Such types are essentially comparable with modern breeds of dogs. Our purpose

TABLE 1

General information concerning dove crosses from which significant numbers of offspring were obtained

Races crossed	No. of matings for F_1	Direction of cross	Persistence	Inbreeding after F_2	Maintained or became extinct
72 × 62	3 {2 1	♂72 ♂62	F_9 F_2	Moderate	Maintained
72 × 63	10 {8 2	♂72 ♂63	F_{9+}	Slight	Maintained
72 × NA	9 {5 4	♂NA ♂72	F_{11+}	Moderate to slight	Maintained*
72 × 67	4	♂67	F_7	Slight	Maintained*
72 × 51	4	♂72	F_3	Moderate	Maintained
72 × 206	2 {1 1	♂72 ♂206	F_6	Moderate to slight	Extinct
72 × OT	4 {2 2	♂72 ♂OT	F_{10}	Moderate to slight	Maintained
72 × 75	8 {5 3	♂72 ♂75	F_5	Moderate to slight	Maintained
72 × 36	7	♂36	F_7	Moderate to slight	Maintained
72 × N2	4	♂72	F_1 only	....	Extinct*
63 × 62	6 {4 2	♂62 ♂63	F_6	Moderate	Maintained
63 × 51	2 {1 1	♂63 ♂51	F_6	Moderate	Maintained
63 × 44	1	♂44	F_8	Intense to moderate	Extinct*
62 × 11	1	♂11	F_7	Moderate	Extinct
62 × 75	3	♂62	F_9	Slight	Maintained
62 × N2	4 {3 1	♂N2 ♂62	F_8	Slight	Maintained*
62 × 36	2	♂36	F_6	Slight	Extinct
62 × B	3 {2 1	♂B ♂62	F_4	Slight	Extinct
N2 × OT	1	♂N2	F_4	Intense to moderate	Extinct
N2 × 44	1	♂44	F_{10}	Moderate to intense	Extinct
N2 × NE	1	♂NE	F_6	Intense	Extinct
B × 36	2	♂36	F_5	Slight to moderate	Maintained
B × 75	2 {1 1	♂B ♂75	F_6	Moderate	Maintained

*Considerable numbers of young offspring were used in other studies.

in including such races in the study was much the same as that of Stockard,[7] who undertook, after the present study was started, an examination of the endocrine status of some of the various breeds of dogs. It seemed that the concurrent breeding of several varieties of domestic pigeons on the same spot and under identical conditions—together with attention to such items as age at maturity, reproductive performance, and data for size and functioning of endocrine organs and processes—should provide important information. At the outset it was not entirely clear whether the great disparity of body size in those races would prove a help or a hindrance as regards the objectives of the present study.

A second group of types, somewhat similar to our dove races, was formed, in addition, within our own colony and studied concurrently with the well defined racial types referred to above. Most of these heterogeneous types were already more or less established before 1921, when we began to take weights and measurements of their endocrine organs. One or two of these types, however, were not well fixed and inbred either then or later because, in these cases, it seemed more important to perpetuate two interesting mutations (ataxia and "scraggly" plumage). It seems necessary to describe these several types and races. Those types formed in our own breeding pens will be described first.

Types Formed in Our Own Colony

Race *267* was a mixture of the Jacobin and Fantail breeds with ordinary domestic pigeons. The Jacobin contributed about three-fourths and the Fantail about one-eighth of the total inheritance. These birds were characterized by medium-small stature, rather long and loose plumage, and pied ash-red color; many of the birds had a feather whorl (crest) on the head, had extra tail feathers, and were without a uropygial gland. The stock was inbred closely, when once started as a race, except in the fifth generation, when first cousins once removed had to be used to perpetuate the line. Extinction occurred in the ninth generation, largely from sterility of the males (see study of their testes). A true hermaphrodite appeared in this race, and in a cross with another race (Tippler = *T*) the hereditary tendency was preserved to form a "hermaphrodite-producing race" (*T* × *267*) which still exists in fair numbers. A further statement concerning these particular hybrids will be found in chapter 10.

Race *SA-E* (= scraggly-ataxia—early) originated from two birds almost exclusively. These birds were an ataxic (mutant) female obtained in 1914 and a scraggly (mutant) male reared in 1915 (both from C. O. Whitman stock). The race derived from this pair included many perfectly normal birds, but a continual segregation of the two mutant characters occurred. The inheritance of these mutations has been reported by Riddle[8] and by Riddle and Hollander,[9] who showed that both are simple recessive conditions. The two ancestral birds were slightly related and were of mongrelized, partly Homer, ancestry. The general appearance of these birds and their offspring was like that of most common pigeons seen in city parks, and their color was generally slaty (wild type) with various patterns, and occasionally some piebaldness and "opal." This stock was maintained for nine generations, with only moderate or little inbreeding after the second generation (only occasional sib matings).

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[7] Stockard, C. R., The genetic and endocrine basis for differences in form and behavior (Amer. Anat. Mem., no. 19: Wistar Inst., Philadelphia, 1941).

[8] Riddle, O., Proc. Soc. Exper. Biol. and Med., 1918, vol. 15, p. 56.

[9] Riddle, O., and W. F. Hollander, Jour. Hered., 1943, vol. 34, p. 167.

Race *SA-R* (= scraggly-ataxia—recent) was obtained by mixing race *SA-E* with a female of race *299* and then backcrossing to *SA-E*. The resulting stock was maintained with a moderate amount of inbreeding, and both ataxic and scraggly individuals frequently segregated out. The "opal" color occasionally appeared, as well as some piebald and white individuals, and "smoky." After about seven or eight generations (when a depletion of females threatened the maintenance of the stock) an outcross was made to Homers, and this was followed by backcrosses, repeated four times, to *SA-R*. The resulting stock is still maintained, although piebald specimens have been eliminated.

Race *299* was derived from a rather large white female (probably a Runt or White King) and a male which was approximately half Jacobin and half mongrel type. The majority of the descendants were of medium-large structure and had rather long, loose white plumage. They were inbred quite intensely and became extinct, after much mortality, in the sixth generation.

An attempt was made to establish and maintain three additional types of pigeons, but this was not successful enough to warrant consideration of data obtained from any of them. These types were lost early. No attempt was made in pigeons to select individuals or generations for size of any endocrine organ.

Standard Races

Most of the birds used as foundation for the standard stocks were obtained from exhibitors of the respective breeds at the annual poultry shows in New York. Particulars concerning these races are given below. Throughout this study it has frequently been found convenient to substitute a letter (*M*, *T*, *H*, etc.) for the proper name of these races.

The Magpie race (*M*) is a well known breed having a rangy, or elongated, body structure. Our stock derived from 7 birds, but nearly all birds used in the present study were derived from 2 pairs. Intensive inbreeding (sib matings) was practiced except when less close inbreeding was necessary to maintain the stock; extinction (of males) occurred in the seventh generation. The birds of this population were medium small, with quite long neck, limbs, and beak. Because of their tall and slender build these birds were always regarded as the "Scandinavians" of our colony. Their color, a quite constant character, was the typical pied, black-and-white pattern. The plumage of this breed has a glossy sheen, apparently associated with a defective ("greasy quill") condition of the fluff feathers of the body. These birds, above all others utilized in this study, were shy and fearful of people, and they were not very active sexually.

The Tippler race (*T*) is well known as one of the smallest of the fancy breeds.

Many breeders keep and use Tipplers for the sport of endurance flying. Our stock derived from 2 pairs. Occasionally, but not consistently, this stock was intensively inbred, and it is still well maintained after fifteen generations. The typical specimen is small, trim, with short beak and toes, "pearl" iris, and sometimes slight coloboma. The plumage colors are either wild type, grizzled, dilute, or a combination of these colors.

The Homer (*H*) is the well known message-carrying pigeon, but it exists in more than one variety. Our stock was derived largely from 7 birds, and in their offspring inbreeding was often (not always) intense. The stock was carried for about nine generations and then discontinued. The strain name of the particular Homers of our colony is unknown. In fact, it seems probable that some Fantail was represented in their ancestry, since extra tail feathers, absence of uropygial gland, and prominent forehead were frequently noted in the offspring. Attempts to fly and "home" this stock were disappointing, even at distances of one or two miles.

Another strain of Homers (*HC*), quite distinct from the above, was maintained from a single pair contributed by Dr. Lee S. Crandall, curator of birds at the Bronx Zoological Park, New York City. This stock was inbred rather intensely and became extinct in the sixth generation. These birds were much heavier than the more usual type (*H*), and they showed a more exaggerated development of "ceres" of beak and eyelids. As nearly as this point can be determined, the type is known to breeders as the "Show Racer" (not the "Show Homer"). The plumage was about the same as that of the other Homers in length and appearance, but the birds themselves were much larger. Plumage colors were wild type and checkered.

The Carneau (*C*) is a very large "utility" breed. The variety used was the White Carneau, obtained from Mr. Wendell M. Levi, of Sumter, South Carolina. Little or no inbreeding has been practiced, and in this single instance the data which will be presented for the race were obtained partly from purchased birds and only partly from specimens reared in our own colony.

The White King (*WK*) is an extremely large "utility" breed, almost indistinguishable in superficial appearance from the White Carneau, but having a different origin. Our stock was established from 2 pairs of purchased birds. Inbreeding was often though not always intense. The stock was acquired late and was studied only to the sixth generation. This population was uniformly white with dark eyes. An occasional specimen showed a growth of degenerate "stub" feathers on the toes.

The Runt (*R*) is a large, long-feathered breed, which is probably represented in the remote ancestry of both the Carneau and the White King. Three birds (2 males and 1 female) were the origin of our stock. They were probably inferior to the breed average in size, and their offspring were not as large on the average as either Carneaux or White Kings. Their descendants were inbred intensely, with few exceptions, and the stock became extinct in the seventh generation. The plumage colors were of two types, wild type and brown.

TYPES OF HYBRIDS OBTAINED FROM PIGEON CROSSES

From the 11 races of pigeons listed above, 16 hybrid types were obtained. Not all these crosses produced sufficient numbers of healthy young to supply a significant body of data. In most cases, however, F_1, F_2, and later generations have been studied. Certain items relating to these several hybrid types are recorded in table 2. One of the types requires the following additional statement.

A very large population was obtained from crosses between Tipplers and race

TABLE 2

GENERAL INFORMATION CONCERNING PIGEON CROSSES FROM WHICH SIGNIFICANT NUMBERS OF OFFSPRING WERE OBTAINED

Races crossed	No. of matings or F_1	Direction of cross	Persistence	Inbreeding after F_2	Maintained or became extinct
T × 267	9 {2 7	♂T ♂267	F_{15}	Slight	Maintained*
T × SA-E	6 {1 5	♂T ♂SA-E	F_4 F_7	Intense Moderate	Extinct
T × M	8 {2 6	♂T ♂M	F_{12}	Moderate to slight	Maintained*
T × H	4 {2 2	♂T ♂H	F_6	Moderate	Extinct*
T × R	1	♂T	F_8	Slight	Maintained
M × 267	2	♂M	F_3	Intense	Extinct
M × SA-E	4 {1 3	♂M ♂SA-E	F_3	Intense	Extinct
M × 299	1	♂M	F_5	Intense	Extinct
M × R	4 {2 2	♂M ♂R	F_7	Intense to moderate	Extinct
267 × SA-E	2	♂SA-E	F_4	Intense to moderate	Extinct
267 × H	3 {1 2	♂267 ♂H	F_6 F_4	Intense	Extinct
R × SA-E	5 {2 3	♂R ♂SA-E	F_8	Moderate	Extinct
R × 299	5 {1 4	♂R ♂299	F_5 F_3	Moderate	Extinct
R × H	5 {3 2	♂R ♂H	F_5	Moderate	Extinct*
R × HC	2	♂R	F_{10}	Moderate to slight	Maintained
WK × H	1	♂H	F_3	Intense	Extinct

*Considerable numbers of young offspring were used in supplementary studies.

267 (hybrids = $T \times 267$). This cross was made repeatedly; 9 matings were made for F_1 offspring. After F_2, inbreeding was only occasional, and the stock has been maintained readily, even beyond the fifteenth generation. In this population all birds are rather small, and the internal bony structures often give an impression of delicacy—of smallness or of fragility. On the other hand, the plumage often seems rather long. The parental plumage colors, crest, and other characters are randomly distributed among the population. The point of greatest interest about this population, however, is its hermaphroditism. A case of true hermaphroditism was first noted in this stock, but facts obtained soon thereafter indicate that race 267 carried the genetic factors which are responsible for this condition. This abnormality has been selected for in recent generations; and some success, at least in increasing the frequency of its occurrence, has attended these efforts. This population is now, and more properly, regarded as a distinct race, a "hermaphrodite-producing race."

Photographs of Runts, Homers, and Magpies are reproduced in plate 3. Some of the particular birds represented in the ancestry of pigeon races are shown in plate 4. Other individuals which are representative of races and hybrid types as they appeared at the conclusion of the study are shown in plate 5.

THE ENVIRONMENT AND DISEASES OF DOVES AND PIGEONS DURING THE TWENTY-FOUR YEARS OF THE TEST

The elements of the environment which have greatest importance in the physiology of both doves and pigeons are feed, caging conditions, disease-producing organisms, and seasonal changes (temperature and light). It is necessary to record several facts concerning these elements of the environment.

Diet

Since measurement of thyroid size during a long term of years was a major goal of the present study, it was fully realized that the maintenance of an essentially constant food and water supply was of first importance to successful study of the problem. Indeed, doves and pigeons seemed especially adapted to this test since these birds apparently require only dry grains for continued sustenance, and it seemed probable that the same (or a quite similar) grain mixture could be obtained indefinitely. If these experimental animals had required fruit or fresh vegetables, which vary with season in source, kind, and quality, this study, at least the part relating to the thyroids, would not have been undertaken.

The grain mixture employed throughout most of the period contained the following grains in the proportions noted:

For pigeons	*For ring doves*
150 lbs. cracked yellow corn	200 lbs. cracked yellow corn
200 lbs. wheat	200 lbs. wheat
150 lbs. Kafir (or milo)	100 lbs. Kafir (or milo)
100 lbs. hemp	75 lbs. hemp
	100 lbs. canary seed
	100 lbs. millet

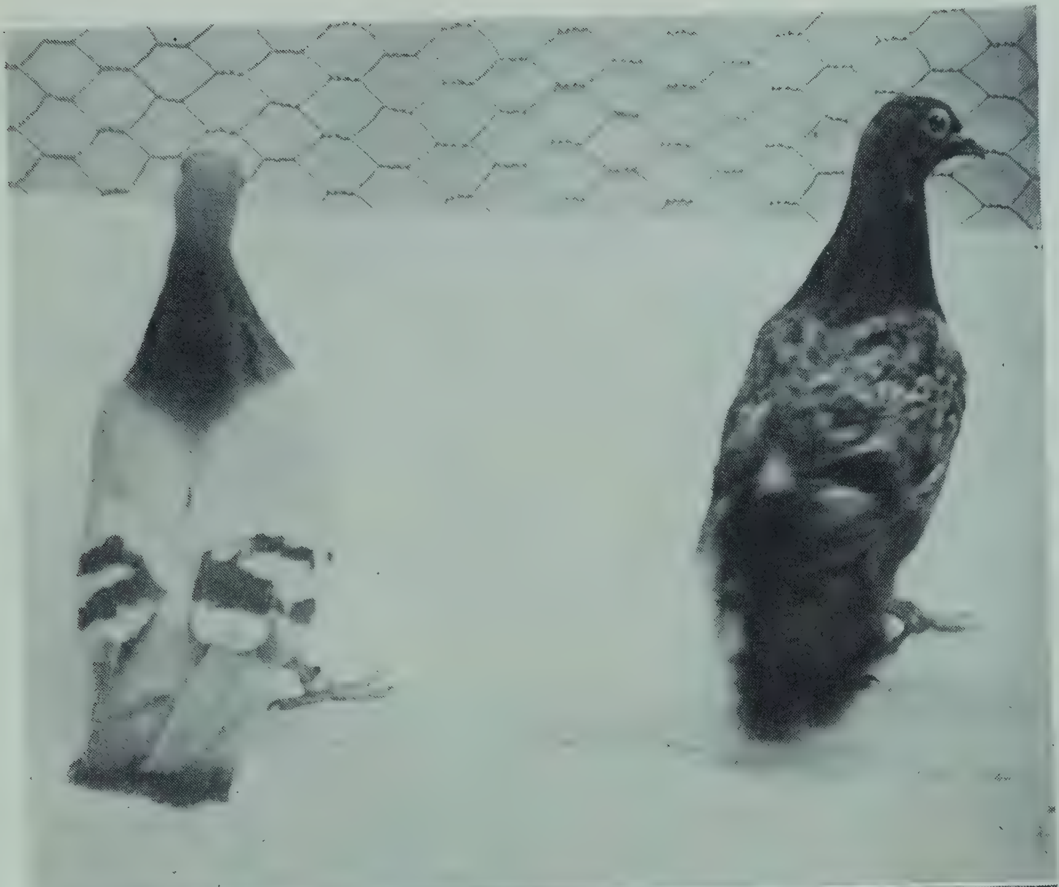
PLATE 4

Four birds represented in the ancestry of certain pigeon races or types established in this colony and included in the present study.

Above. The ataxic (♀ 151; at left) and "scraggly" (♂ A126; at right) individuals which provided most of the ancestry of races *SA-E* and *SA-R*.

Below. A Jacobin (♂ A445; at left) which contributed to the ancestry of races *267*, (*T* × *267*), *299*, *133*, and *SA-R*. A Homer-type mongrel (♀ A442; at right) which, as mate of the Jacobin, contributed to the ancestry of the above-named races.

PLATE 4



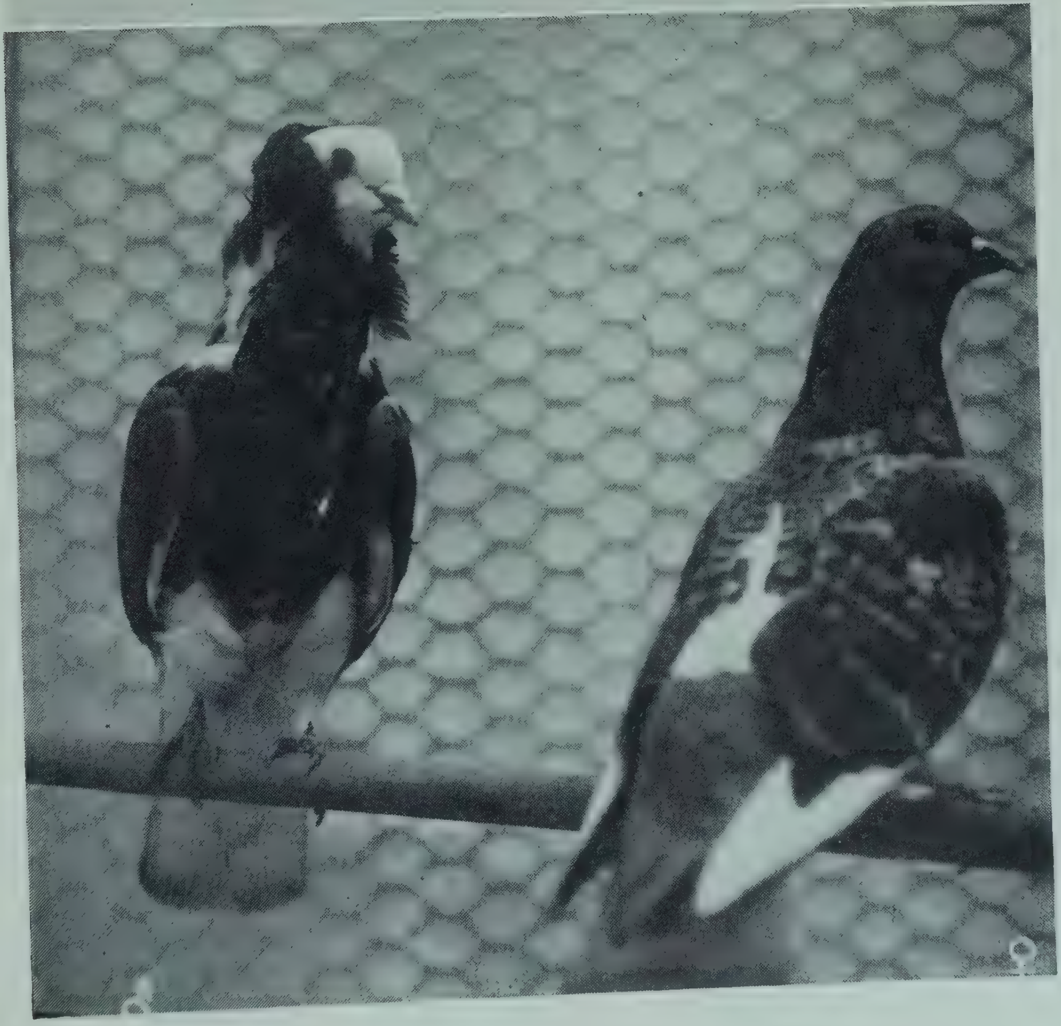


PLATE 5

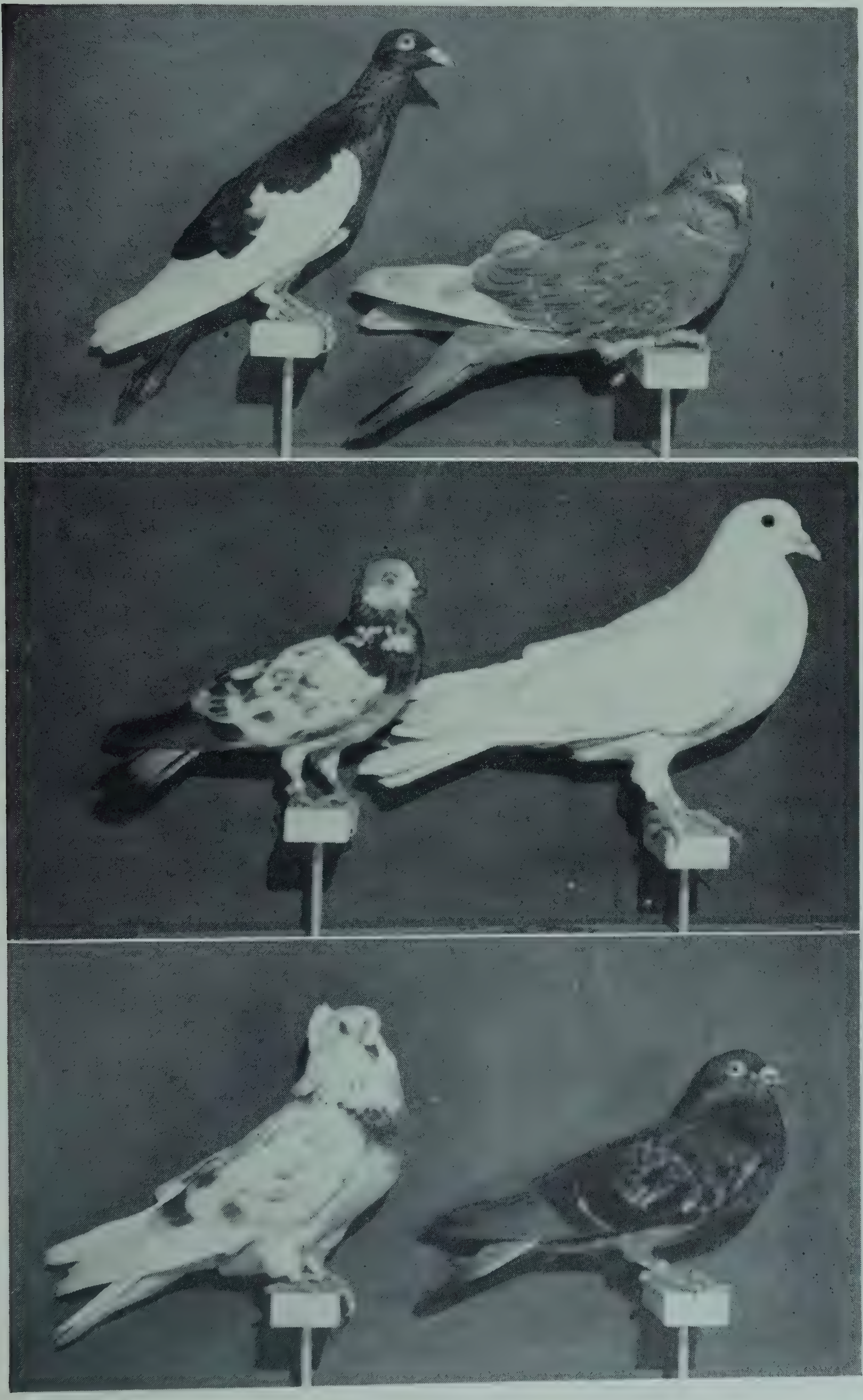
Representatives of certain pigeon races and hybrids at the end of the test. All males, photographed March 1945.

Above. A Magpie (at left), blind, aged 13 years. A Runt × Homer *C* hybrid (at right).

Center. A Tippler (at left), smallest of pigeon races used. A White Carneau (at right).

Below. A Tippler × 267 hybrid ("hermaphrodite-producing race"; at left). A "normal" (not ataxic or scraggly) of race *SA-R* (at right).

PLATE 5



In the final 3 years of the test (1942 to 1944, inclusive), however, hemp and canary seed were discontinued because of their unavailability or excessive cost; thereafter both Kafir and milo were used, and in amounts sufficient to replace the hemp and canary seed. During the terminal 7 years hemp was displaced by peas in the diet of pigeons, and the proportions of the various grains varied somewhat from time to time. None of the grains used were grown locally, and their source probably varied considerably during the 24-year period.

The mineral supply (always available in excess) consisted at first of cuttlefish bone, cracked oyster shell, grit (crushed granite or marble), wood charcoal, and rock salt. From 1937 onward, however, these elements were replaced by a commercial grit mixture containing oyster shell, calcite, bone meal, charcoal, coarse sand, salt, and iron oxide (Fe_2O_3). Throughout these tests coarse sand (frequently renewed) from the same local source covered the floor of the cages. Ring doves were supplied with water from an identical source (a driven well) throughout the period of the tests. For pigeons aged 2 months to (or somewhat after) sexual maturity, during the years 1917 to 1930 only, water was supplied from a surface spring. Pigeons of other ages were at all times supplied with water from a driven well.

It is to be noted that although supplementary vitamins were not given to this colony of birds during a period of at least 34 years, the diet seems to have been essentially adequate for these species. It is possible, however, that these races could have been better or more easily maintained through the use of vitamin supplements. The young (2 months old to maturity) of pigeons were usually reared in direct sunlight in very large cages. Doves were reared in medium-sized cages (1.2 × 2 × 2 m.) but not often exposed to direct sunlight during the coldest months (November to April); during the winter they were immediately behind large glass windows in good light and were given access to outdoors during the warmer part of only a few days. These conditions of lighting apparently enabled all or most birds to produce adequate amounts of vitamin D. After maturity some pairs of breeding birds were somewhat less exposed to direct sunlight, especially in winter.

Diseases

Parasites and other disease-producing organisms were continuously present in some individuals of the colony. Mites and lice have usually, though not quite always, been successfully combated by individual treatment of birds and by sterilization of nest boxes and nest-building material. Worm infestations, by *Ascaridia columbae* and *Capillaria columbae*, were the most troublesome and persistent disorders (particularly in doves). Other diseases were "canker," caused by the protozoan *Trichomonas;* tuberculosis; paratyphoid, caused by *Salmonella typhi-murium;* ulcerative enteritis, probably caused by *Corynebacterium perdicum;* and, in pigeons, an unidentified disease which seemed to be fatal within a few days and which produced a marked lengthening and thinning of the intestine. Tests of several serum samples by Dr. K. F. Mayer (complement fixation reaction), in 1942, were positive for psittacosis. We have been unable to diagnose this disease, however, and are not sure whether it has any significance in these studies. Satisfactory diagnosis of many cases of enlargement of the liver and spleen, sometimes accompanied by fatal hemorrhage from these organs, was not achieved.

The hygienic and health conditions of the several generations of birds used in this study are better described as average than as ideal. The floors of the cages were cleaned at intervals of 1 to 2 months, and covered with a layer of fresh sand. This condition permits some transmission of worm eggs and bacteria, especially in periods of dampness.

Season

Extreme changes associated with season and temperature produced changes in the birds used in this study. It was early learned that the thyroids of doves and pigeons show an increase in weight during the autumn and winter.[10] For this and practical reasons the killing of birds to obtain their organ weights was distributed over the twelve months of the year, and much effort was continually directed toward an even distribution of the killing of the available birds of the various races at the four seasons of the year. These birds, however, were not exposed to the full rigors of winter. Maturing pigeons were able to divide their time between outdoors and indoors (some heat) in winter; all breeding pairs were kept indoors (some heat) in winter. Maturing doves were kept indoors in winter in buildings which were supplied with more heat; pairs of breeding doves were similarly protected but were confined in smaller cages than were used for large groups of immature doves. Artificial heating was supplied from November to April. The glass sides of their houses were completely removed from early May to late October or early November. During the autumn, however, all doves and pigeons were exposed to air with great cooling power (winds); and in winter, though all breeding pairs were protected from moving air, the temperature occasionally fell to the freezing point.

Miscellaneous Factors

All these races have been bred continuously at the same spot, 4 or 5 m. above sea level, and differences due to altitude and climate are excluded as agents capable of explaining differences observed in measurements made on these several races. Excepting those birds which were used as starting points for the various races, nearly all individuals have been killed (or died) before they attained advanced age; most birds were aged 6 to 30 months when killed to obtain the weights of their organs. The thyroid glands of old birds (they may live to 100 months or more) in our colony are known to be somewhat larger than those of young (mature) birds.[11] Since individuals of the several races were given ample, and essentially equal, opportunity for exercise and flight, it is very improbable that any of the racial or hybrid differences observed in this study are traceable either to close confinement or to a variable degree of confinement.

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[10] Riddle, O., and W. S. Fisher, Amer. Jour. Physiol., 1925, vol. 72, p. 464.

[11] Riddle, O., Amer. Naturalist, 1929, vol. 63, p. 385.

Many doves and pigeons were hatched, fed, and reared in nests of foster parents. In general, these foster parents were somewhat less inbred than the birds whose eggs they adopted. This procedure permitted the rearing of greater numbers of young from valuable parents than would have been possible otherwise. But in addition to its practical value, this procedure has other implications. At least some individuals of each race and hybrid type were reared by foster parents of a different genetic type. Thus, the extinction of valuable races or hybrid types did not depend (or depend solely) upon the circumstance that certain pairs of parents were poor incubators and feeders; such pairs were indeed sometimes obtained, but after this was detected their eggs were usually transferred promptly to other pairs. On the whole, the rearing of some young by foster parents tended to equalize certain aspects of the environment that could be equalized perhaps in no other way.

One condition of change which is applicable to pigeons, but not to doves, must be recorded though it may seem trivial. When the two colony houses used for pigeon breeding (labeled 4 and 5 in the frontispiece to this volume) were built (1916), they seemed too much exposed to the heat of summer sunshine. Therefore the growth of some very small saplings, which annually produced more and more shade for the pigeons, was encouraged. It is perhaps possible that the progressive reduction of direct summer sunlight by these trees was related to the increased weights of the thyroid glands of pigeons in the years following 1930. Turner[12] seems to have demonstrated that deprivation of ultraviolet light is a powerful goitrogenic agent in growing Barred Rock fowl.

Measurements and Autopsies

Weights and measurements were made on several organs of all birds (except many emaciated dead birds) aged more than 3 months. The body weight was taken immediately before the bird was killed by decapitation. The desanguination which accompanied this method of killing prevented the inclusion of large amounts of blood in the weights assigned to the various organs. Weights of internal organs were taken immediately after killing and desanguination. The abdominal organs—the liver, spleen, gonads, and oviduct—were weighed first. The intestine, from the lower margin of the gizzard to the anus, was then cut out, and all its mesenteric folds teased apart completely with the fingers. It was then laid out straight on a meter stick, but without stretching, and measured to the nearest centimeter. Thereafter the thoracic cavity was opened and the right and left thyroids were removed; these were carefully trimmed of excess fat and connective tissue and quickly weighed on an analytical balance. Finally, the weight of the heart was obtained.

Frankly pathological conditions observed either at autopsy or in previous daily inspections were recorded. After its length was measured, the intestine was slit open or otherwise examined for the presence of worms. When *Ascaridia* were present they were counted and their number was recorded. The size and general appearance of the adrenals, thymus, and pancreas were regularly recorded.

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[12] Turner, K. B., Proc. Soc. Exper. Biol. and Med., 1930, vol. 28, p. 204.

In the analyses of data presented in this volume the birds have been grouped usually in two (or three) health classes. In such groupings, "H" designates birds which were regarded as quite healthy, "A" includes otherwise healthy birds parasitized by *Ascaridia* (any number), and "D" includes birds which died or showed disease when sacrificed for study; in general, data from birds of class D are wholly disregarded. In many summaries it has been found possible to combine data from classes H and A, since in these particular cases significant differences either were not found or were quite infrequent.

Statistical Procedures

Much consideration was given to the question of a suitable method for the presentation of the diverse data assembled in part I of this volume. This resulted in a decision to use percentile analysis of frequency distributions. The percentile method, as noted by Boyd,[13] has the advantage of simplicity and completeness, and is more logical than other methods in dealing with highly skewed distributions. The data are distributed into classes, or actually plotted, and the median (50 per cent of the values to the right and 50 per cent to the left) and the quartiles (25 per cent of the values, Q_3 above and Q_1 below the median, respectively) are located. The extreme deciles (10 per cent of the values, at each end of the range) are also used for populations of 50 or more individuals. Each population is graphically represented by a straight line, showing the extreme range. On the line the median is indicated by a diamond, the quartiles by crossbars, and the extreme deciles by half-bars placed above the line. Examples may be found in most chapters of part I. This pictorial or graphic method of presentation is a partial adaptation of a method introduced by Hubbs[14] and discussed elsewhere by Hollander.[15] A series of comparable populations can thus be viewed against the same scale.

For a simple measure of deviation in the population, use is made of the quartile average, $Q = (Q_3 - Q_1)/2$. The coefficient of dispersion, C.D., is Q/median. The probable error, P.E., of the median is $Q/\sqrt{N} - 1$ (N = total number of values in the population). It is also possible to use χ^2 tests in comparing two populations for significance of differences (Boyd); this has not been done here, however, because of the enormous amount of labor it would entail. Significance has generally been judged on the basis of probable errors, and of the general character of the distributions, and also on the basis of consistency of supposedly comparable populations ("repeatability").

Ratios of ♀/♂, and organ-weight percentages of body weight, are calculated simply as ratios of the respective medians. Probable errors of these ratios, used chiefly in the case of heart-weight analysis, are calculated as follows (a represents one measure, e.g., heart, and b another, e.g., body; it is assumed that there is no correlation between a and b):

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[13] Boyd, E., Anat. Rec., 1935, vol. 62, p. 1.

[14] Hubbs, C. L., and A. Perlmutter, Amer. Naturalist, 1942, vol. 76, p. 582.

[15] Hollander, W. F., Amer. Naturalist, 1946, vol. 80, p. 494.

$$\text{P.E. of ratio } a/b = \frac{\text{C.D. of } a + \text{C.D. of } b \times \text{ratio } a/b}{\sqrt{N} - 1}$$

Correlations have been calculated by Spearman's method in a few instances, but more often they have been estimated from careful examinations of scatter diagrams. It will be noted later that correlations of organ weight with body weight are generally low (or nonexistent) within a race; when all races are combined as the population, however, these correlations are high.

In the case of dove thyroid weights (and in one group of data for age at sexual maturity in females), where time graphs are necessary, "moving medians" (and other percentiles) were calculated to smooth the curves. This method, like that for "moving averages," uses the data for three successive intervals combined to obtain median, etc., for the middle interval; then, one advances an interval and again combines three. On graphs of dove thyroids the first and last medians are based on only two intervals in order to retain the full length of the curves.

Questions concerning the calculation and tabulation of data for heat production are discussed in connection with the presentation of those data in part II.

2

BODY WEIGHT IN DOVE AND PIGEON RACES AND IN HYBRIDS

Neither body weight, as such, nor the mode of its inheritance was a matter of primary interest in the present study. Various organ weights, measurements, and reactions are related, however, to body weight, and it is necessary therefore to provide an analysis of the body weights of the various racial and hybrid types. Some data on the inheritance of body size were obtained automatically from the racial crosses. Outside the present volume, few data for body weight are available for ring doves. For pigeon races body weight is a little better known, but since very few of the known breeds were included in this study it seems advisable to refer at once to this information and to certain studies that have been made on the inheritance of body size.

Body Size and Its Inheritance

Using pigeons exhibited at a pigeon show in Copenhagen, Wriedt and Christie[1] obtained body weights of 458 individuals belonging to 23 breeds. Two of those breeds, Magpies and Runts, were also used by us. The exhibited Magpies had an average body weight of 380 gm. and the Runts averaged 818 gm.; the largest specimen of the latter breed weighed 1225 gm., and an African Owl weighed only 225 gm. Although breeders of Runts place emphasis on heavy specimens, it is probable that our stock of Runts was of somewhat inferior body weight from the beginning. Wriedt and Christie observed that Fantails and Jacobins had keel bones which were short in relation to their body weight (the latter breed was partly represented in our races *299* and *SA-R;* both breeds contributed to races *267* and *T* × *267*). Keel length was considered a more satisfactory measure of size than weight. Concerning this point it may be noted that although it is doubtless true that the keel is subject to less physiological fluctuation than is body weight, there are two objections to its preferential use as a measure of body size. First, it is in fact merely a part of the skeleton, and may vary independently of other parts of the skeleton. Second, it is a less sensitive measure of increase in general body size than is weight; the data of Wriedt and Christie show that body weight increases about three times as fast as does keel length.

Wexelsen[2] concluded the study on size inheritance begun by Wriedt and Christie; he ignored body weight in favor of keel length. No evidence for sex linkage of size factors was found in this study; in general, the inheritance seemed to involve at least two or more factors. Specific leg-length and beak-length factors were indicated as well as factors for general body size. Studies on the inheritance of body weight in other domestic birds are neither numerous nor very extensive, but multiple-factor inheritance is indicated in all cases hitherto reported.[3] A multiple-factor basis for the inheritance of body size in mammals has also been established. A marked maternal influence has apparently been observed, however, in certain mammalian hybrids.[4]

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[1] Wriedt, C., and W. Christie, Ztschr. f. indukt. Abstam.- u. Vererbungsl., 1926, vol. 42, p. 93.

[2] Wexelsen, H., Jour. Exper. Zool., 1937, vol. 76, p. 161.

Heterosis in animals is very rarely connected with increased size. An exception was noted by Gates[5] in hybrids between the Japanese waltzing mouse and the house mouse. Neither inbreeding nor crossing in poultry has been observed to affect body size notably,[6] and it is a well known fact among breeders of pigeons that body size and "vigor" are not interdependent.

Although growth rate in various breeds or races may not seem an important part of our present subject, the following items are believed to constitute part of a background of significant information. Data obtained chiefly on races utilized in the present study (but excluding all highly specialized races such as Tipplers, Magpies, and Runts) indicated that at about 2.5 months after hatching, doves and pigeons have attained about 90 per cent of their ultimate body weight.[7] Thus these animals are unusual in that nearly all their growth is attained very early, and a plateau for body size is apparently maintained indefinitely. In a study of growth rate in a large series of animals, Brody,[8] utilizing the above-cited data of Riddle, concluded that, of the species he examined, the pigeon and dove attain their mature weight most rapidly, and that their adult weight is highest in relation to the time required to reach it.

Still another study[9] was made on relative growth rates on four of the pigeon races used in the present work. Those races were Tipplers, Magpies (small), Homers (intermediate or large), and Runts (large). Weights were obtained at several periods between hatching and 87 days thereafter. The weights of the newly hatched embryos of these four races demonstrated that racial size difference was only partially expressed by size differences attained during embryonic life; this difference was fully attained, however, by further differential growth rate within 20 days after hatching.[10]

[3] Jull, M. A., and J. P. Quinn, Jour. Hered., 1931, vol. 22, p. 283; Maw, A. J. G., Sci. Agric., 1935, vol. 16, p. 85.

[4] Walton, A., and J. Hammond, Proc. Roy. Soc. (London), B, 1938, vol. 125, p. 311; Castle, W. E., W. H. Gates, S. C. Reed, and L. W. Law, Genetics, 1936, vol. 21, p. 310; MacArthur, G. W., Amer. Naturalist, 1944, vol. 78, p. 142.

[5] Gates, W. H., Carnegie Inst. Wash. Pub. 337, 1926, p. 83.

[6] Warren, D. C., Kansas Agric. Exper. Sta. Tech. Bull. 52, 1942.

[7] Riddle, O., and P. Frey, Amer. Jour. Physiol., 1925, vol. 71, p. 413; Riddle, O., Amer. Jour. Physiol., 1928, vol. 86, p. 248.

[8] Brody, S., Univ. Missouri Agric. Exper. Sta. Res. Bull. 102, 1927.

[9] Riddle, O., D. R. Charles, and G. E. Cauthen, Proc. Soc. Exper. Biol. and Med., 1932, vol. 29, p. 1216.

[10] In a still larger race, White Carneau, 27 days were required to attain this stage (Bates, R. W., O. Riddle, E. L. Lahr, and J. P. Schooley, Amer. Jour. Physiol., 1937, vol. 119, p. 603).

Endocrine Control of Body Weight

The period of rapid increase of body weight in young pigeons was shown by Schooley and Riddle[11] to occur at a time when eosinophilic pituitary cells are differentiated and apparently active, but *before* the basophilic cells begin to show signs of maturity. In these birds the eosinophils differentiate during the latter part of embryonic life; but basophils begin to mature during the second month after hatching. In this and an earlier study[12] evidence obtained by the implant method indicated that gonadotrophin is absent, and prolactin is present, in the pituitaries of pigeons aged 1.5 months. These studies indicate that basophilic cells (and gonadotrophin) do not play any important part in the pigeon's attainment of its racially determined body weight; but eosinophilic cells (which secrete prolactin) and prolactin are at least present and active at this stage, and thus it is possible that they assist in determining the body weight, and indeed different levels of body weight. Removal of the anterior pituitary gland in young pigeons has been found in this laboratory to be followed by cessation of growth; and the development of supernormal (by 20 to 35 per cent) body weights in doves and pigeons by injections of purified prolactin has been observed repeatedly in this laboratory.

In view of the above-noted tendency to stability of body weight in doves and pigeons after an early age, it seems significant that cyclic changes occur in relation to the reproductive cycle. In these adult birds, males and females alike, Riddle and Braucher[13] observed that the body weight increases by more than 7 per cent during the 15 days (doves) or 18 days (pigeons) spent in the incubation of their eggs. Maximum weight is attained at the end of the incubation period, and nearly one-third of the total increase occurs in the crop sacs, where it is definitely identifiable as a direct and specific response to prolactin. The remainder of the increased weight seemed to occur in the body in general, except in the skeleton, and was believed to have a hormonal basis which in time relations at least is associated with the release of prolactin from the bird's pituitary gland.

Thereafter it was shown experimentally that prolactin increases appetite and body weight in normal[14] and in hypophysectomized[15,16] pigeons. In the two last-mentioned studies it was further found that adrenal cortical hormone likewise assists in the maintenance of normal body weight in both hypophysectomized and adrenalectomized[17] pigeons. Both prolactin and cortical hormone assisted also in the maintenance of liver weight, intestinal length and weight, and weight of the pancreas. Complete maintenance of weight of the pancreas, however, required the further addition of thyroxin or thyrotrophic pituitary hormone. It thus appears that the pituitary gland has multiple relations with maintenance or increase of body weight in pigeons, although this laboratory has observed no evidence that a specific "growth" hormone shares in these effects in doves and pigeons.

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[11] Schooley, J. P., and O. Riddle, Amer. Jour. Anat., 1938, vol. 62, p. 313.

[12] Riddle, O., and J. P. Schooley, Proc. Soc. Exper. Biol. and Med., 1935, vol. 32, p. 1610.

[13] Riddle, O., and P. F. Braucher, Amer. Jour. Physiol., 1934, vol. 107, p. 343.

[14] Bates, R. W., O. Riddle, E. L. Lahr, and J. P. Schooley, Amer. Jour. Physiol., 1937, vol. 119, p. 603.

[15] Schooley, J. P., O. Riddle, and R. W. Bates, Amer. Jour. Anat., 1941, vol. 69, p. 123.

[16] Miller, R. A., and O. Riddle, Endocrinology, 1943, vol. 32, p. 463.

[17] Miller, R. A., and O. Riddle, Proc. Soc. Exper. Biol. and Med., 1943, vol. 52, p. 231.

McCarrison[18] concluded that "in healthy common pigeons the pituitary is considerably heavier in females than in males." Riddle and Nussmann[19] confirmed this result for pigeons and further extended it to ring doves. This last-mentioned study was made on many of the races and hybrid types with which the present research is especially concerned; it was made with special reference to the relation of pituitary size to intestinal length, and the results of the study are fully reported in chapter 5 below. Certain items, however, will be mentioned here since they have bearing on the present consideration of body weight. First of these items was the observation that the anterior lobe of the adult pituitary seems relatively larger per unit of body weight in the larger species (pigeons) than in the smaller species (doves). Again, the available data (not all races were studied) suggested that dove races *75* and *72*, and *72* × *62* hybrids, had unusually large pituitaries (both sexes), whereas races *51* and *62* (both sexes) apparently had relatively small pituitaries in relation to body weight. Magpies apparently had relatively the largest pituitaries among the thirteen types of pigeons examined. Among the different races there was apparently little or no evidence of an association of large pituitaries with long intestines; but the sex (female) having the larger anterior lobes had the longer intestine in (probably) all races. Race *51*, with the smallest pituitaries found in any race, was further characterized by the occurrence of individuals with myoclonus, and apparently also by a body temperature more than 1° C. lower than that of any other race of doves used in this study.

Rost[20] made certain comparisons (size, shape, and histology) of the pituitaries of Runts and Turbits (Möwchen). The body weights of these breeds varied between 668 and 818 gm. and 348 and 423 gm., respectively; their hypophyses were said to average 2.3 mg. and 1.63 mg., respectively. Although the Turbit has the broader skull, its hypophysis was narrower than that of the Runt. The Runt's hypophysis was reported to show a greater proportion of basophilic cells, but since neither sex nor other variables were considered, this difference certainly was not established. The pituitary weights obtained by Rost are surprisingly low in comparison with those obtained by McCarrison and ourselves; their reliability may be questioned.

Since skeletal size is rather highly correlated with body weight, the role of hormones in the development of the skeleton requires mention here. It is widely claimed that "growth" hormone stimulates bone growth.[21] In addition, several investigators have observed bone resorption and premature closure of the epiphyses in rodents and dogs as a result of treatment with estrogen. When Riddle and Dotti[22] showed that estrogens do, and androgens do not, increase the plasma calcium (in normal, hypophysectomized, or thyroidectomized pigeons), they immediately expressed the view that estrogens (and gonadotrophin, through the ovary) provide at least a part of the basis for sex differences in skeleton and stature. They further noted that the monthly sex cycles of women—involving periodic temporary resorption and tendency toward maturation of bone, but with these cycles beginning at unequal ages—may be involved also in the establishment of individual and racial differences. More recently the data which seem to support that view have been published in full.[23] The present data provide no real tests of the truth or usefulness of that view. Wexelsen obtained somewhat smaller average values for skeletal structures in female pigeons. Skeletal sex differences apparently existed in the present material (see chapter 11), and to whatever extent hormones are responsible for such differences they are also probably involved in the body-weight differences observed here. It is to be noted, however, that some of these races showed no sex difference in body weight, and there is evidence that races which show a sex difference tend to attain it quite early in life. Moreover, if several hormones are proved to share directly in bodily growth, it is thus made more probable that several of the multiple genetic factors for inheritance of body size act either upon endocrine organs or to alter the sensitivity of tissues to endocrine products.

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[18] McCarrison, R., Indian Jour. Med. Res., 1919, vol. 6, p. 275.

[19] Riddle, O., and T. C. Nussmann, Anat. Rec., 1933, vol. 57, p. 197.

[20] Rost, H., Ztschr. f. wissensch. Zool., 1939, vol. 152, p. 221.

[21] Freud, J., H. Levie, and D. B. Kroon, Endocrinology, 1939, vol. 56, p. 1; Silberberg, M., and R. Silberberg, Amer. Jour. Pathol., 1939, vol. 15, p. 547; Ray, R. D., H. M. Evans, and H. Becks, Amer. Jour. Pathol., 1941, vol. 17, p. 509.

In this connection two dwarf mutations showing stigmata of endocrine abnormality should be mentioned. Snell[24] described a dwarf mutant type of mouse in which Smith and MacDowell[25] later showed that dwarfing is associated with hereditary deficiency of the eosinophilic pituitary cells and their products (growth hormones?). A lethal dwarf mutation was described by Greene, Hu, and Brown[26] in Polish rabbits. These dwarfs showed abnormalities which were believed to indicate primary pituitary disorder involving both eosinophilic and basophilic cells.

Cretinism is, of course, merely a clinical condition, but the specific ability of thyroid medication to increase the body weight of cretins is an illuminating fact. The cases hitherto cited may serve to indicate that a variety of hormones are probably essential to the attainment and maintenance of "normal" body weight, and that different hereditary factors may operate on different hormone producing cells. Moreover, the special studies conducted on pigeons strongly indicate that in these animals prolactin bears a very special relation to their ability to attain their normal body weight.

The relation between sex and body weight in the various races and hybrids is a complicated subject which, equally with race, has required presentation in numerous graphs. At this point it is necessary to say only that the body weight of males usually exceeds that of females. This was not found to be the case, however, in two races of doves (*44* and *N2*) and in two quite dissimilar races of pigeons (Magpies and White Kings).

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[22] Riddle, O., and L. B. Dotti, Science, 1936, vol. 84, p. 557.

[23] Riddle, O., and L. B. Dotti, Proc. Amer. Philos. Soc., 1945, vol. 89, pp. 499–516.

[24] Snell, G. D., Proc. Nat. Acad. Sci., 1929, vol. 15, p. 733.

[25] Smith, P. E., and E. C. MacDowell, Anat. Rec., 1931, vol. 50, p. 85.

[26] Greene, H. S. N., C. K. Hu, and W. H. Brown, Science, 1934, vol. 79, p. 487.

Data for Dove Races and Hybrids

The doves have no history of selection by breeders for diversity of body weight. Whatever differences appear between races in this study result from other selection or from their "hybrid" origin, and the differences found are not very great. Such differences nevertheless exist, and the data obtained for 21 dove races are surveyed in figure 3. The extremes of body size are represented by races *NA* and *67*. Median body weights for the males of these two races differ by about 25 gm., or about 15 per cent of the heavier race; the medians for the females differ by about 13 gm., or 8 per cent of the heavier race. The most extreme difference between females is observed in races *78* and *6;* here the difference amounts to about 22 gm., or 13 per cent of the heavier race. Coefficients of dispersion, however, have not been large; the greatest is about 0.08 (race *NE* females) and the smallest about 0.03 (race *36* males). Individual differences between healthy doves, more or less regardless of race, are rather striking (lowest about 120 gm., highest about 200 gm.), and it seems quite possible that selection could develop races markedly divergent with respect to body size.

Sex differences are most pronounced in races *72*, *B*, *62* (these with large thyroids), *NE*, and *67*, but absent or insignificant in races *N2*, *44*, *NA*, and *51* (all with small or intermediate thyroids). The greatest difference occurs in race *67* (12 gm., or 7 per cent of the male weight). It may be significant that the races in higher ranges of male body weight tend to show sex difference more consistently than do those races in which the males are smaller. The median body weight of males of all the 10 races with highest (male) body weight is greater by more than 3 times the probable error of the median female body weight; within the 11 races with lowest body weight this relation is found in only 5 cases. This might suggest that there are two independent mechanisms operating to produce altered levels of body weight: one that increases male weight only and another that increases or decreases body weight regardless of sex. It is certainly interesting, and perhaps significant, that races *N2* and *44* do not show a trace of the usual sex difference in body weight and that precisely these two races were characterized by greatest intestinal length.

Percentile analyses of body weight in 18 dove races are given in figures 4 to 9. Data for the sexes are treated separately, and separate classes are also made for healthy (H), for healthy but with ascariasis (A), and for diseased and dead birds (D). The latter group should perhaps be entirely ignored, though their inclusion here permitted the presentation of all the data obtained for these races. Taking all races and both sexes together, the effect of ascariasis on body weight was very slight; in 14 of the possible comparisons body weight was greater in parasitized

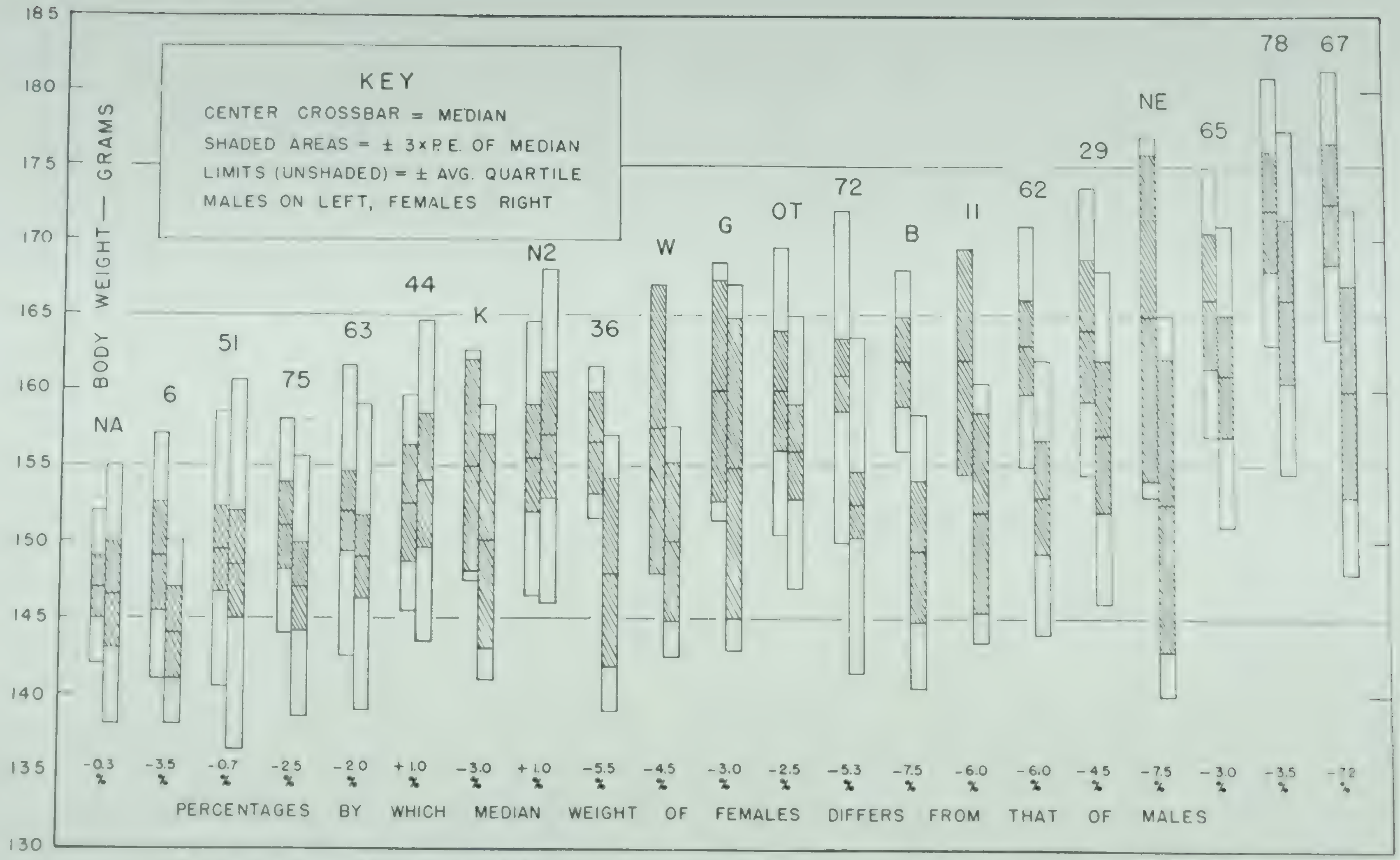


FIG. 3. Graph providing items of information concerning body weight in the two sexes of 21 races of doves

FIG. 4

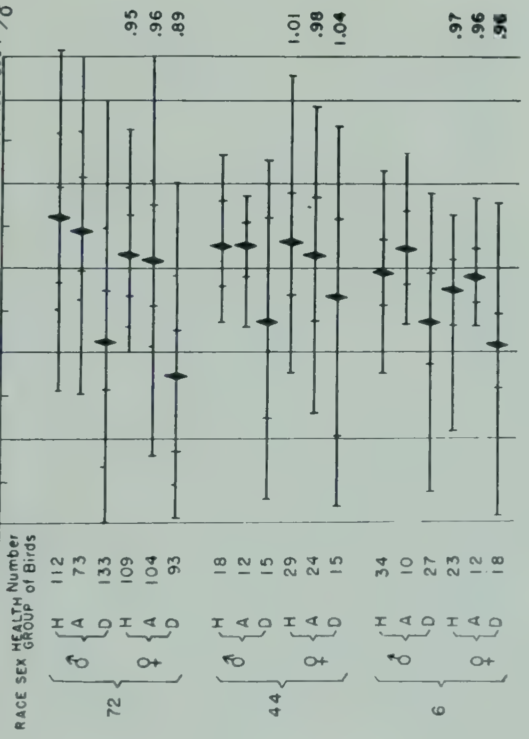


FIG. 5

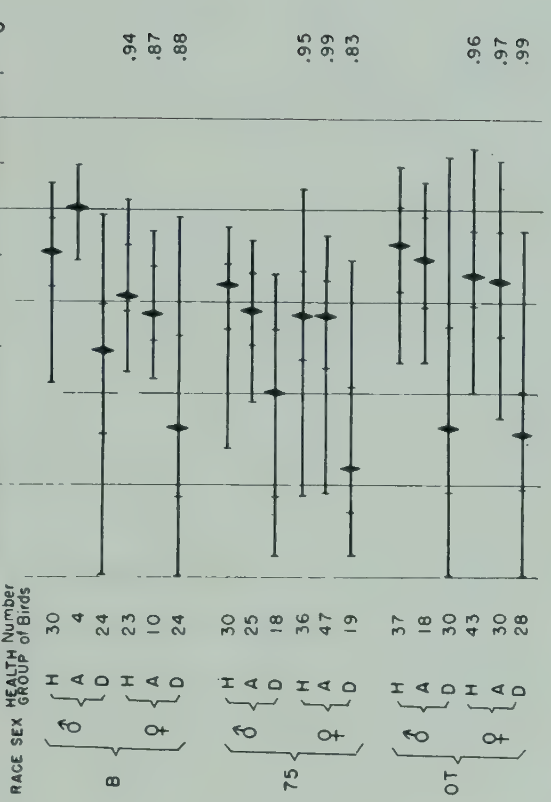


FIG. 6

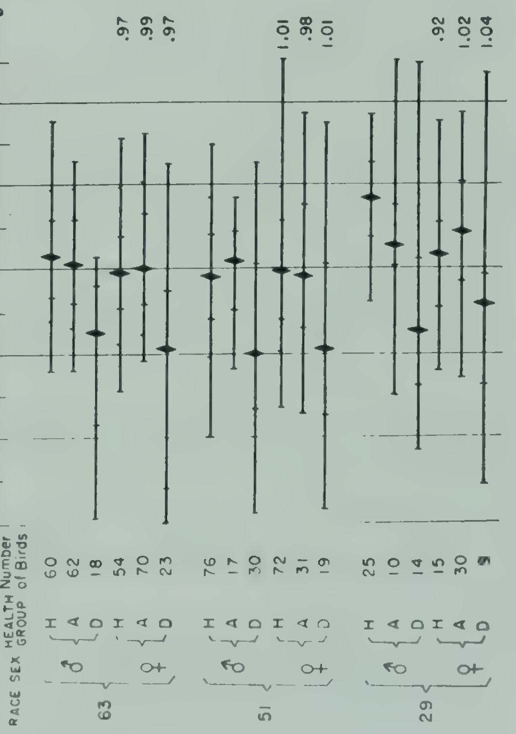


FIG. 7

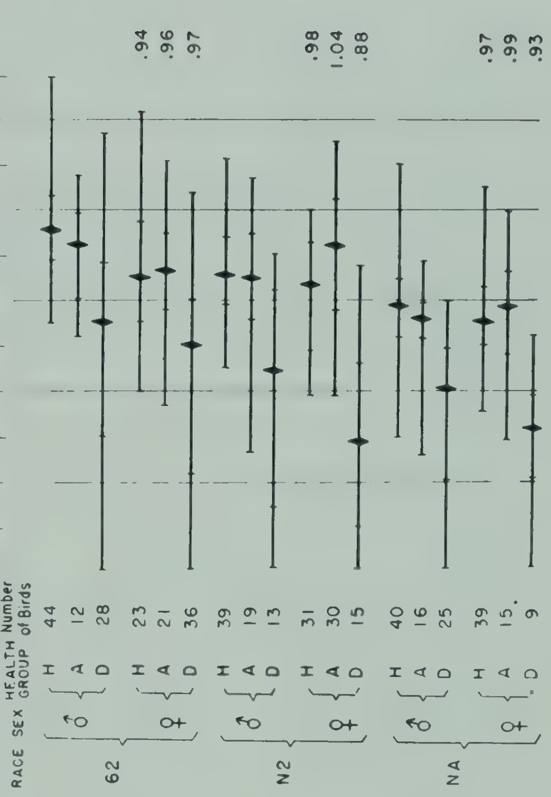


FIG. 8

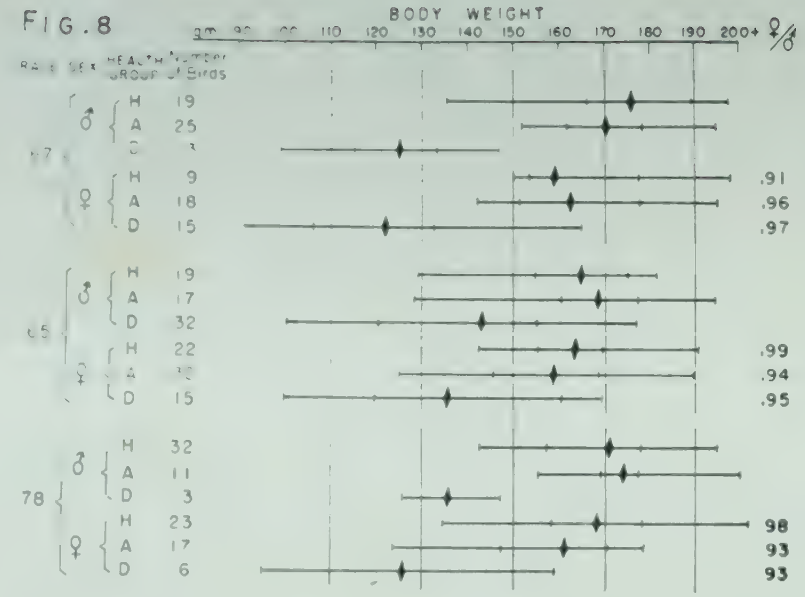


FIG. 9

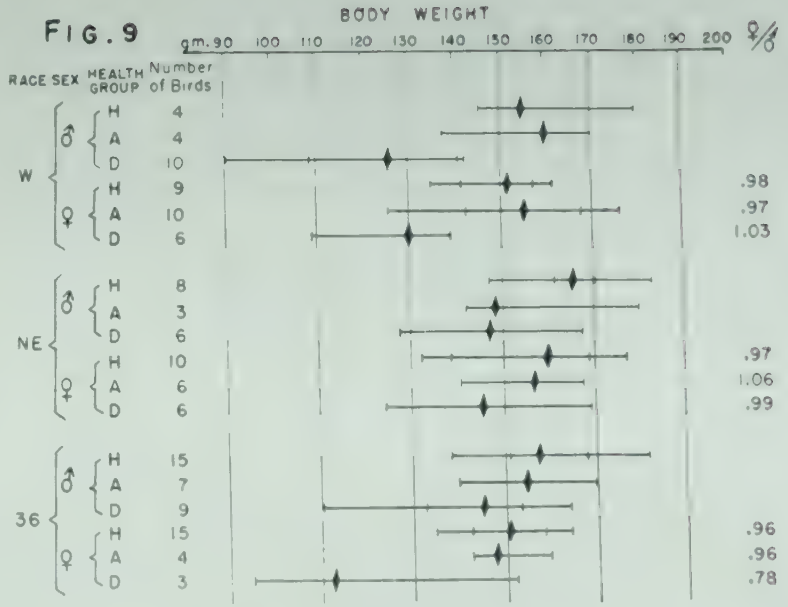


FIG. 10

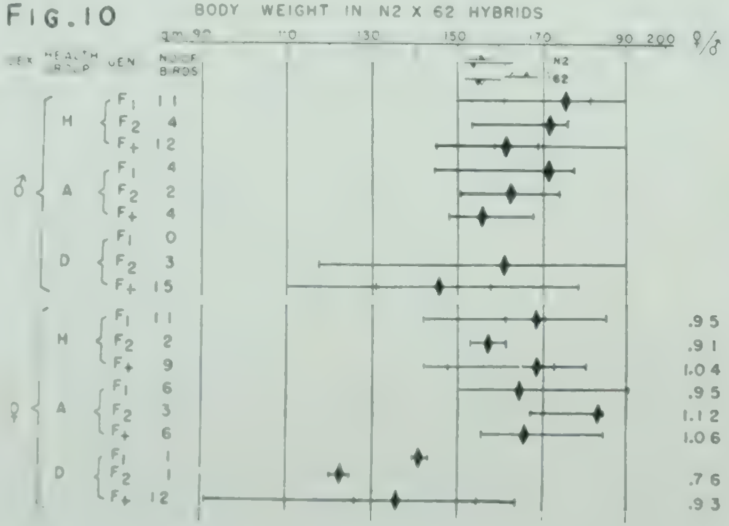
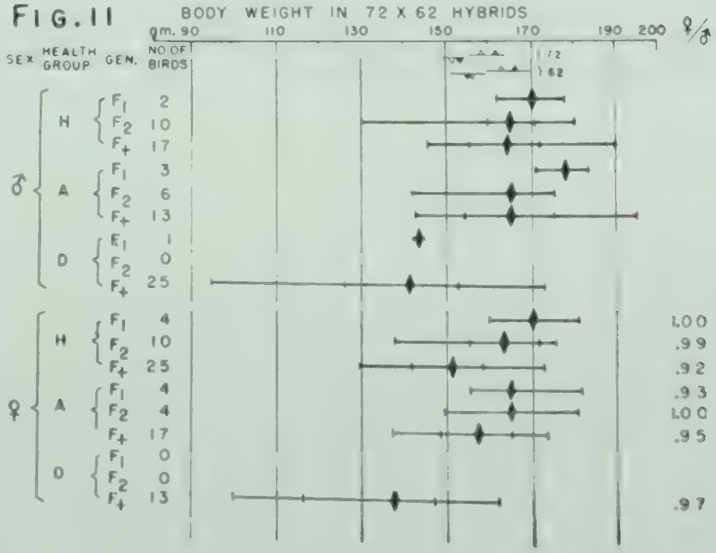


FIG. 11



than in "healthy" groups, in 19 cases it was smaller, and in 3 cases there was no difference. Results within the two sexes were quite similar.

Percentile analyses of body weight in the 7 types of hybrids for which largest numbers are available are given in figures 10 to 16. In order to show possible effects of hybridization, the data for F_1, F_2, and F_+ generations are analyzed separately. At the top of each analysis graphic devices or lines are used to show median values obtained for each sex (males above, females below) of the two parental races; a *solid* half-diamond pointer indicates the median obtained from healthy birds, and a similar *open* pointer marks the median obtained from parental birds with ascariasis. These devices permit easy comparison of data for hybrids with the corresponding median values for the parental races.

The necessary division of F_1 (and F_2) individuals into two sex groups and two health groups greatly restricts the number of individuals treated in each percentile analysis, but any consistency shown by the four groups is not negligible as evidence of similarities to, or departures from, parental body weight. There is definite evidence of heterosis, i.e., of increased body weight, in *N2* × *62* hybrids (fig. 10), and perhaps also in *72* × *62* hybrids (fig. 11). In the other 5 hybrid types, either body weight is apparently intermediate to that of the parent races, or the data are too few to warrant a decision. Thus, crosses of some of these strains did while others did not result in increased body weight. This result parallels Eaton's[27] findings in inbred strains of mice. The F_1 of *NA* × *72* hybrids (fig. 12) shows a sex difference, suggesting that lack of sex difference in race *NA* is recessive. Any simple explanation of inheritance of sex difference seems unlikely, however, in view of the results obtained for *36* × *72* hybrids (fig. 14); here both parental races showed obvious sex difference, but no sex difference was present in the F_1 hybrids. Moreover, in *N2* × *44* hybrids (not shown) there is a tendency to sex difference in all hybrid generations although neither parental race showed this sex difference.

Data for Pigeon Races and Hybrids

A survey of data obtained for the two sexes of 11 pigeon races is provided in figure 17. These races tend to fall into two size groups, or perhaps into three if Tipplers alone may be regarded as a group. This triple grouping holds fairly true for pigeon breeds generally, though the gaps between groups can be bridged by a few breeds and by crossing. Coefficients of dispersion in the data for pigeons tend to be a little larger than for doves; the smallest is 0.05 for females of race *267*, and the largest is 0.11 for White King females. These values for dispersion are quite similar to those for the data of Wriedt and Christie. Ascariasis did not significantly affect body weight.

Sex differences in breeds of pigeons (figs. 18–21) are usually slightly larger than in doves, but none was found in Magpies and White Kings. The greatest sex difference is found in Homers *C*, where it is 12 per cent of the median weight of

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[27] Eaton, O. N., Jour. Hered., 1941, vol. 32, p. 393.

FIG. 12

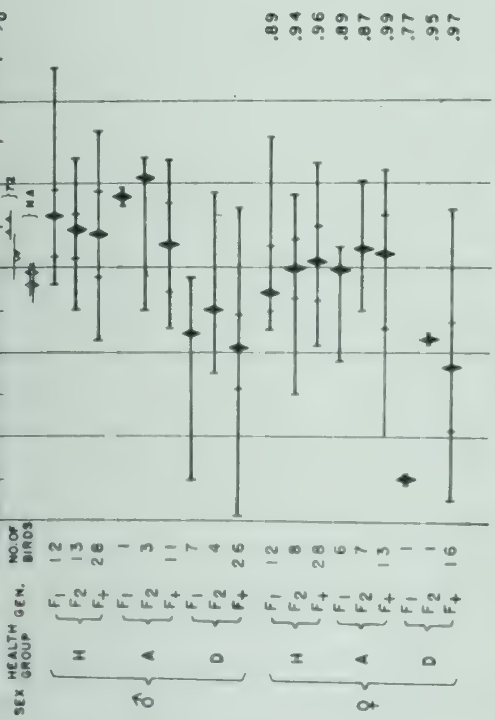


FIG. 13

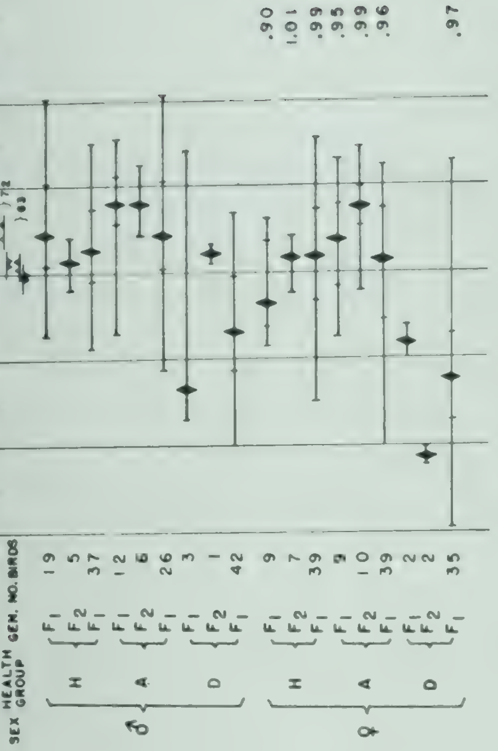


FIG. 14

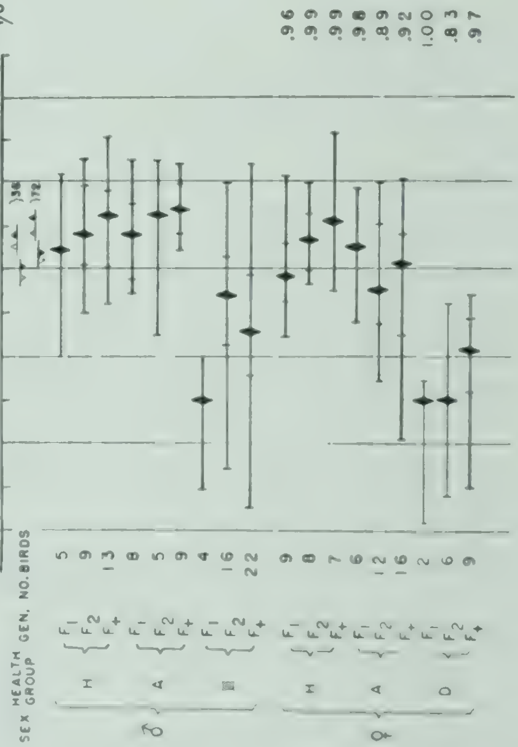


FIG. 15

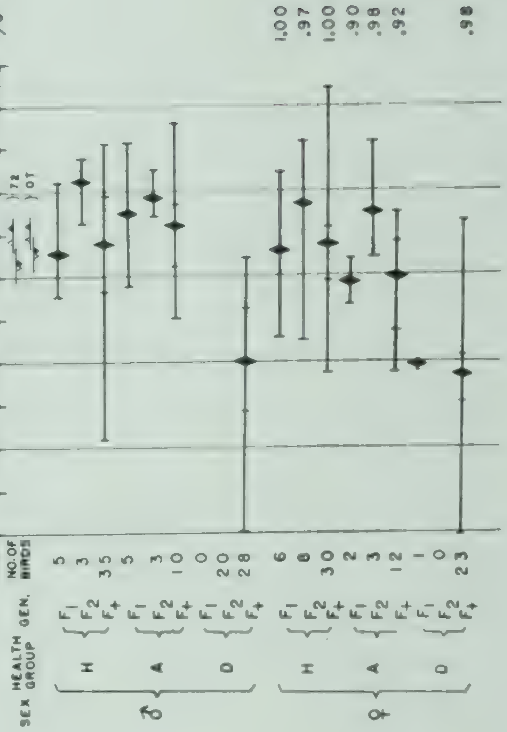
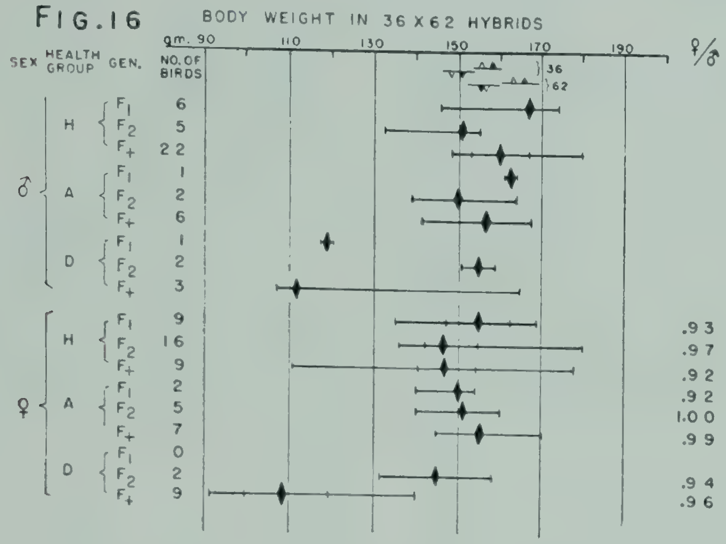


FIG. 16



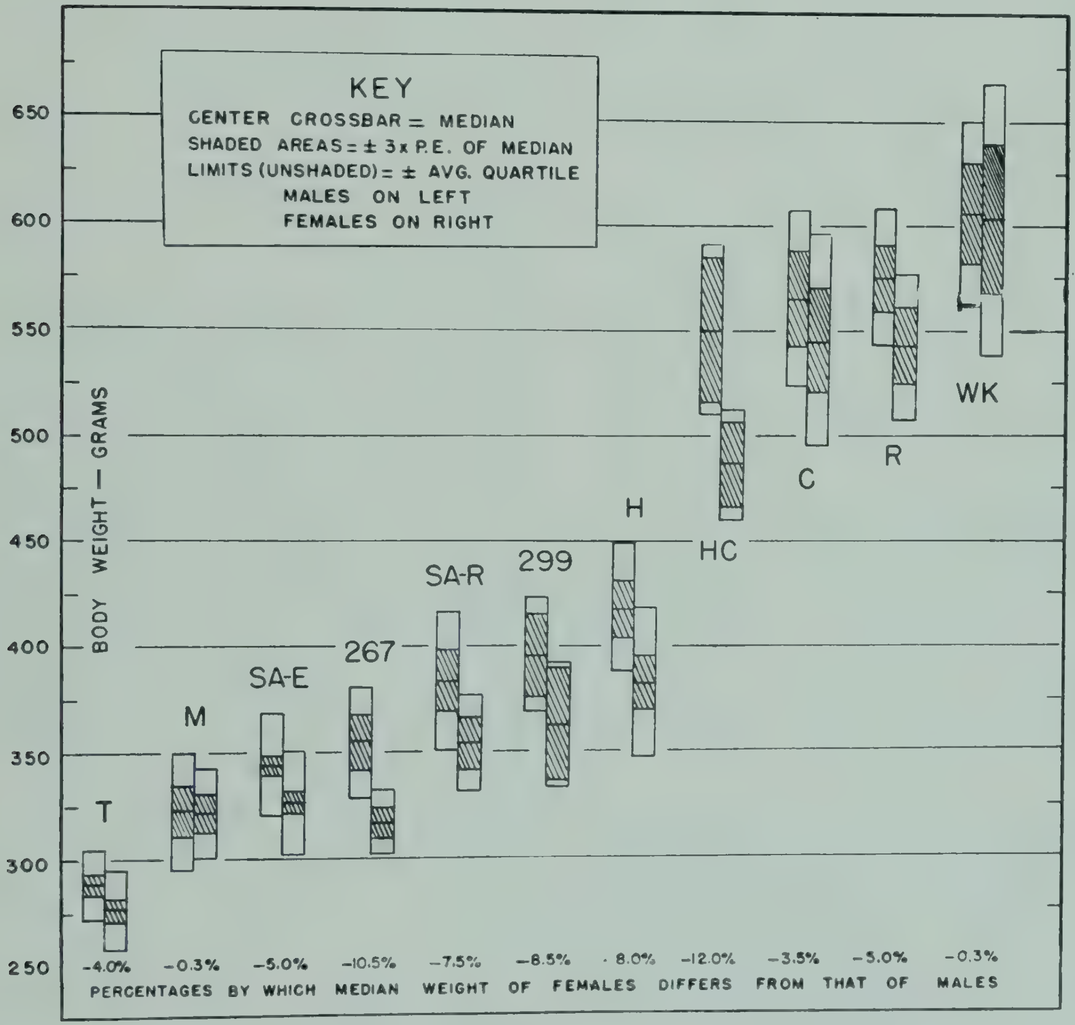


FIG. 17. Graph providing items of information concerning body weight in the two sexes of 11 races of pigeons.

FIG. 18

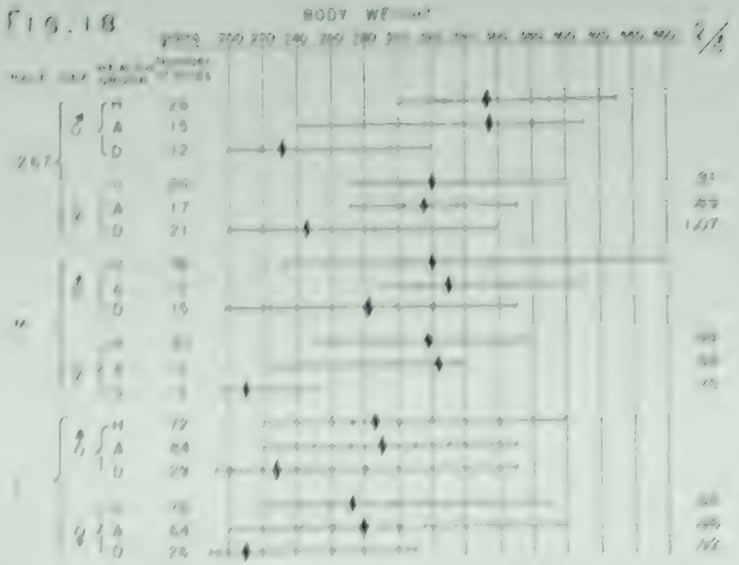


FIG. 19

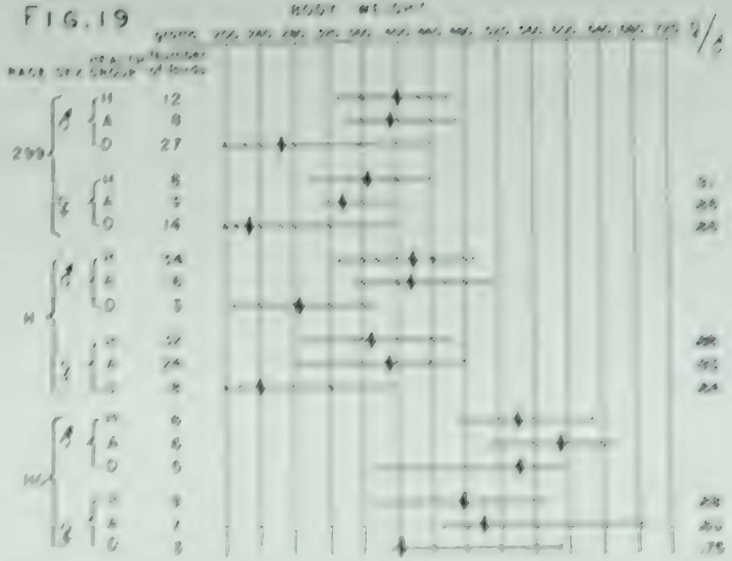


FIG. 20

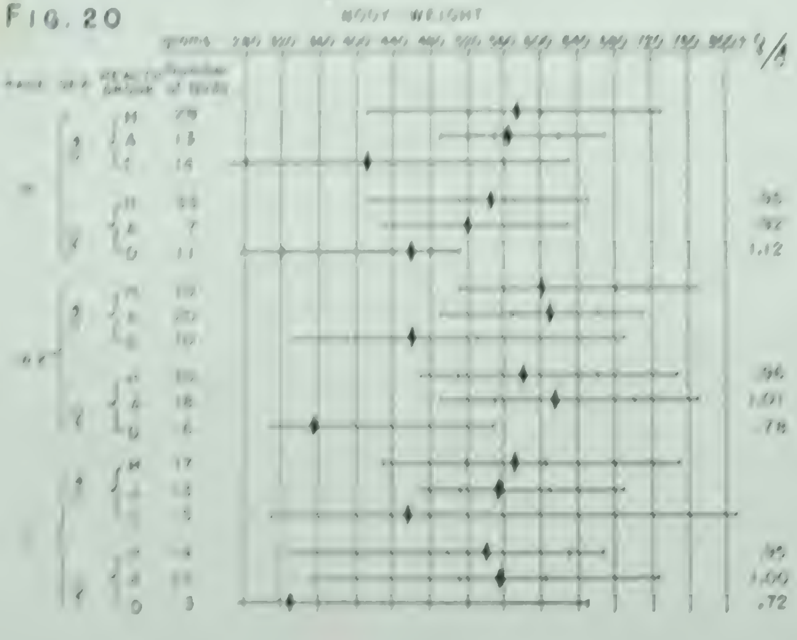


FIG. 21

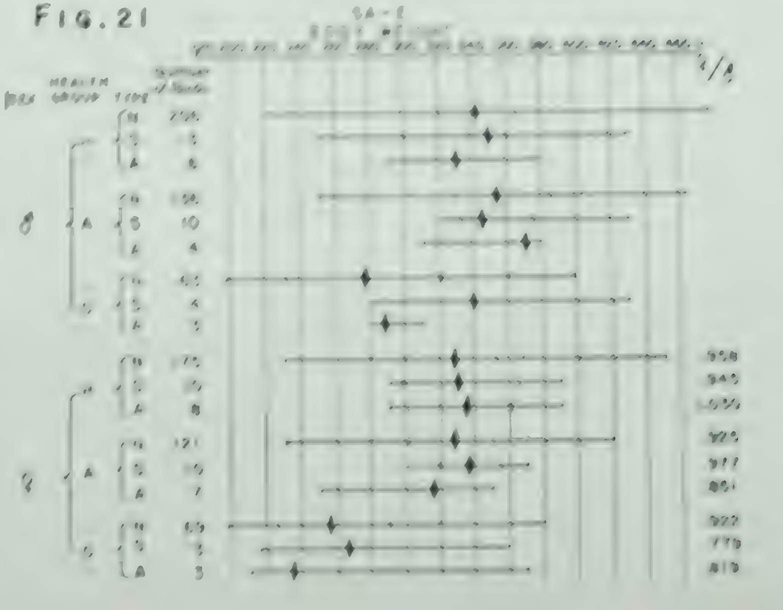


FIG. 22

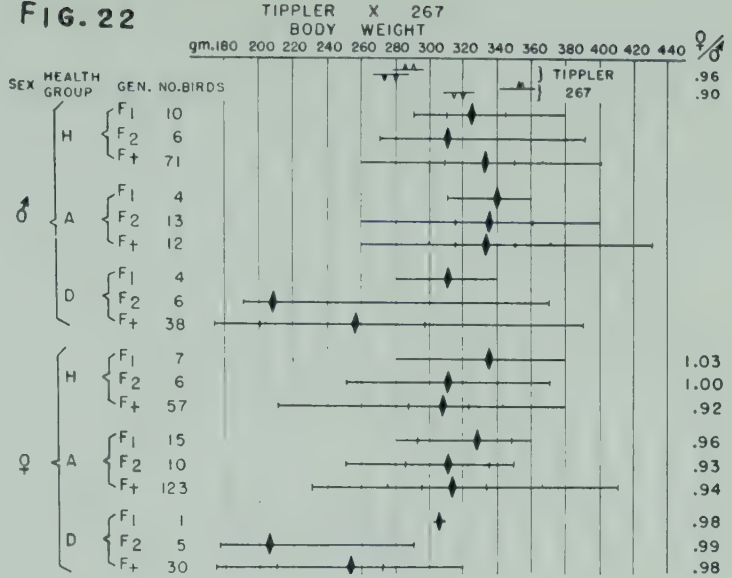


FIG. 23

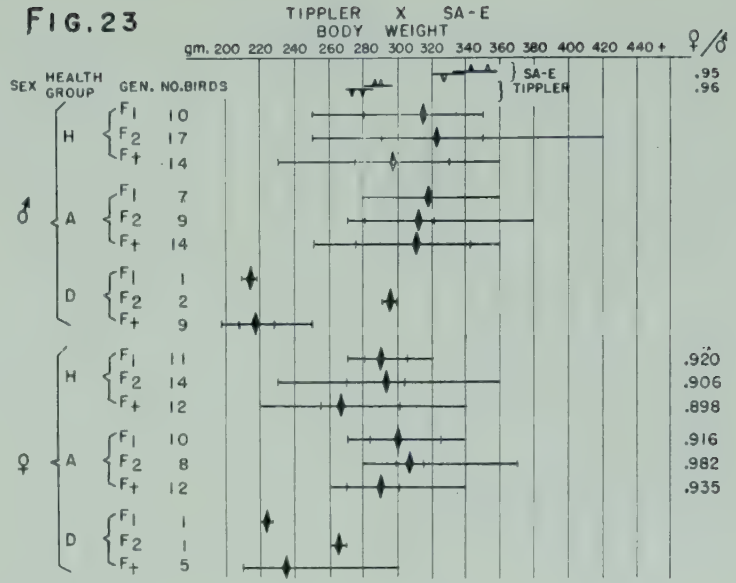


FIG. 24

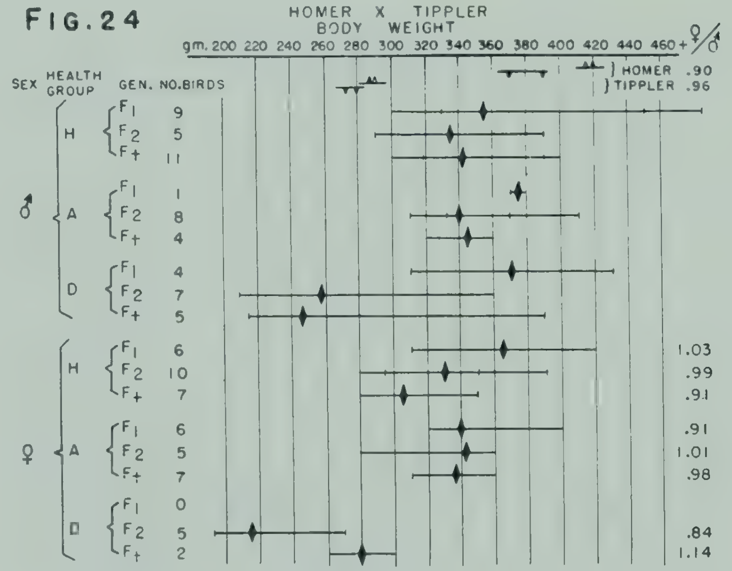


FIG. 25

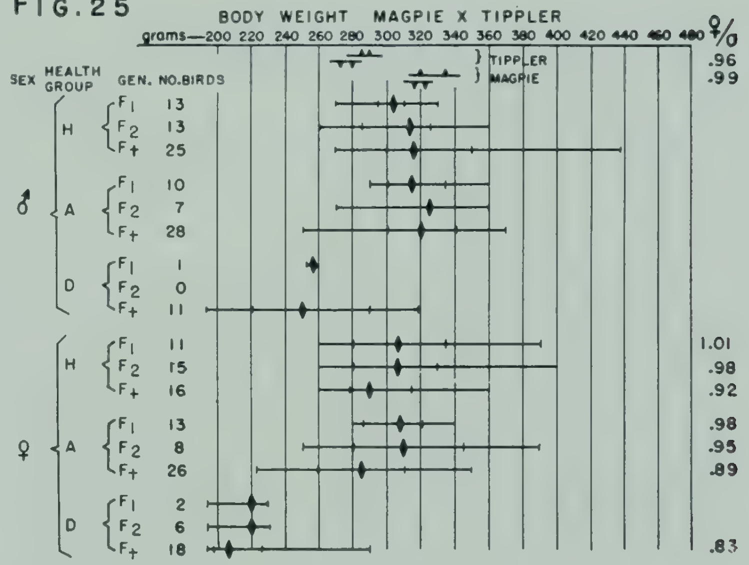


FIG. 26

HYBRIDS, RUNT X HOMER
BODY WEIGHT

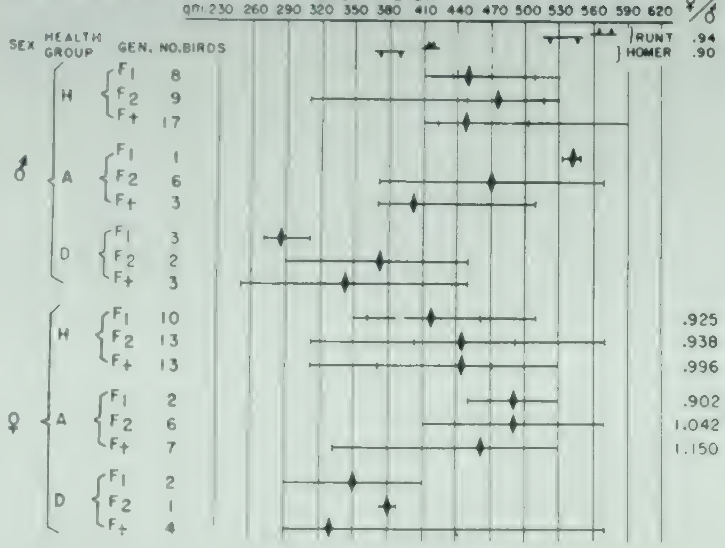


FIG. 27

HYBRIDS, RUNT X 299
BODY WEIGHT

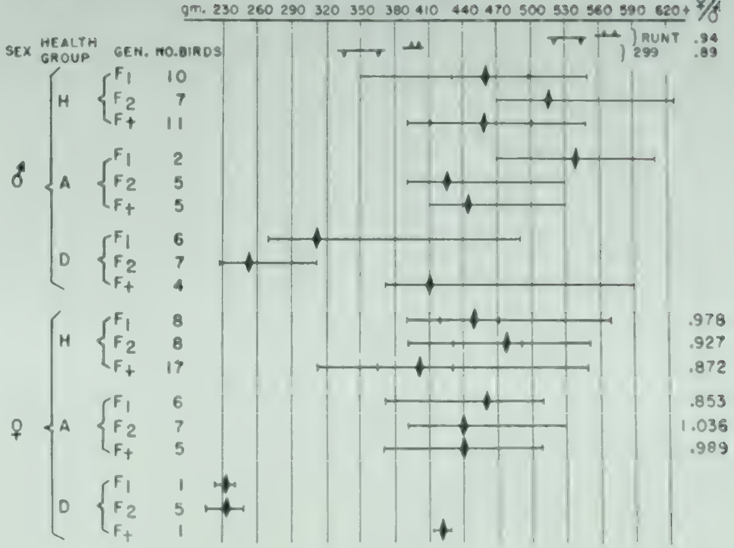


FIG. 28

RUNT X HOMER C
BODY WEIGHT

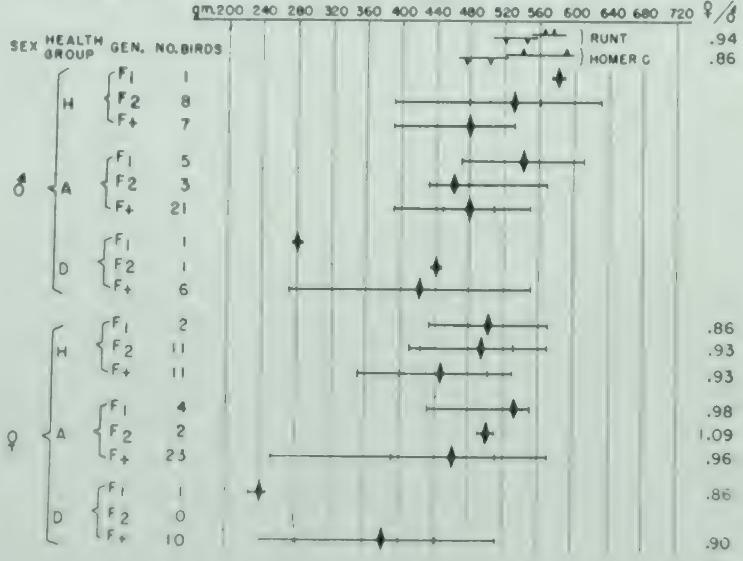


FIG. 29

HYBRIDS, RUNT X SA-E
BODY WEIGHT

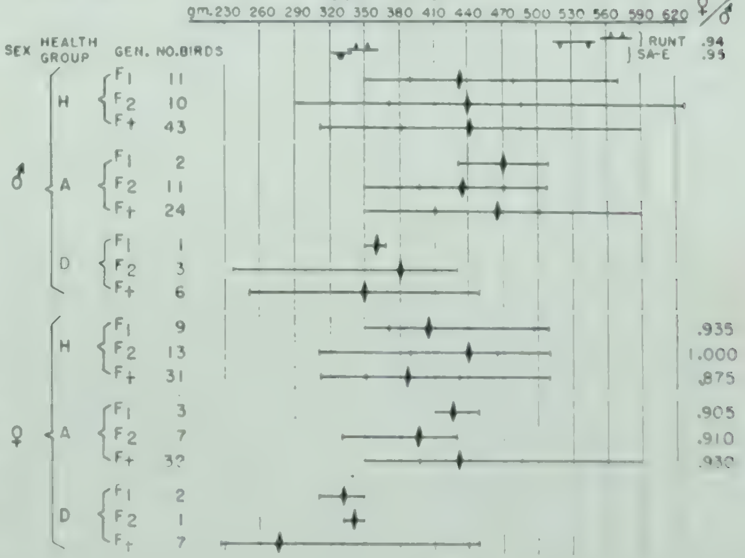
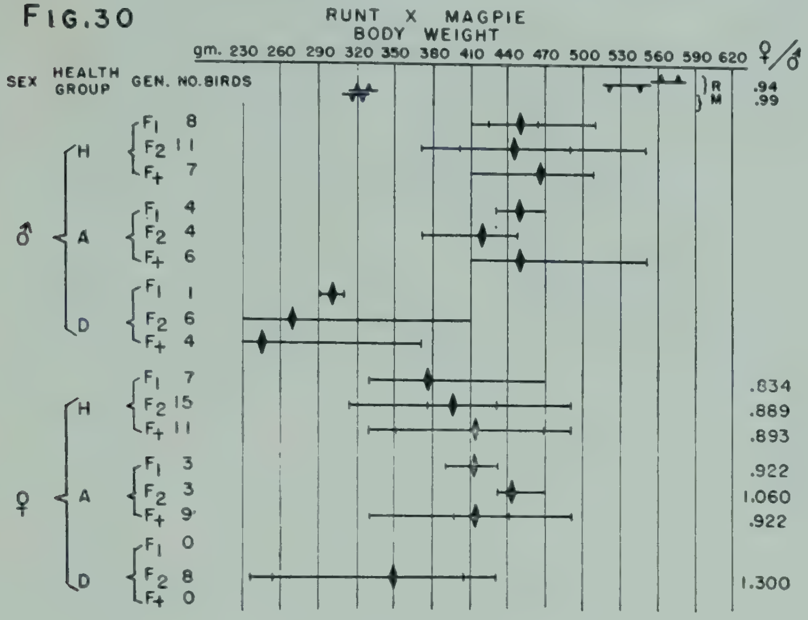


FIG.30



the male. The double mechanism for size alteration suggested above for doves seems equally applicable to pigeons.

In the pigeon hybrids (figs. 22–30) body weight was quite generally intermediate to that of the parental types, with no definite cases of heterotic increase except in *T* × *267* females (fig. 22). In this particular cross both parental races showed fairly clear-cut sex difference, but the F_1 hybrids showed much less sex difference. The heterosis of the females and the reduced sex difference could both be accounted for by a specific increase in the weight of females. The values given for F_+ of *T* × *267* hybrids also constitute the actual measurements of body weight in a population which is elsewhere described as the "hermaphrodite-producing race."

The inheritance of sex difference in body size is as difficult to analyze in pigeons as it is in doves. In addition to the result with *T* × *267* hybrids, just mentioned, there are other peculiar results. In the hybrids *M* × *SA-E* (not shown) and *R* × *M* (fig. 30), one parental type (*M*) shows no sex difference; the F_1 from both crosses show a striking sex difference. On the other hand, the *M* × *T* hybrids (fig. 25) show no significant sex difference in F_1. Larger populations from reciprocal crosses, separately analyzed, would doubtless have provided more definite information on this question.

CONCLUSIONS AND SUMMARY

Doves and pigeons normally attain 80 to 90 per cent of their adult body weight with extraordinary speed—within 3 or 4 weeks after hatching. In all the four cases (pigeons) originally studied with regard to this point, racial differences in body weight attained their full expression within 3 weeks. Perhaps some of the races not included in that study attain characteristically higher levels of body weight through prolongation of this period of rapid growth; in a subsequent study on a very large breed, Carneau, this period was observed to extend to 27 days.

During this short phase of rapid growth, within which the hereditarily determined level of body weight is fully expressed, the eosinophilic cells of the pituitary are active and the basophilic cells are immature and apparently inactive. The pituitaries of these immature birds have been shown to contain prolactin, but they do not contain gonadotrophin in amounts detectable by the implant method.

Much evidence indicates that prolactin exerts a specific role in the attainment of normal body weight in all doves and pigeons. There is as yet no evidence that difference in prolactin production exists in different races, nor that it is causally associated with racially determined body weight. This lack of evidence does not imply negation of such an association. Probably still other hormones are specifically concerned in the attainment of normal body weight in all doves and pigeons, and probably the genetic factors for body weight operate largely through or upon endocrine function.

It does not seem probable that sex difference in body weight in pigeons arises as a result of the action of gonadotrophin on estrogen-producing cells (general theory of Riddle and Dotti), since the difference is often observable in early prepuberal life and since it never develops in certain races.

An incomplete study of weights of pituitary glands of several (not all) of these dove and pigeon races indicated relatively larger anterior pituitaries in females than in males of 27 out of 28 types examined. Relative pituitary size tended to be slightly greater in types of the larger species (pigeons) than in those of the smaller species (doves). Largest relative pituitary size in pigeons was observed in Magpies; races *75*, *72*, and *B* showed largest pituitary size in doves. Race *51* apparently had lowest absolute and relative pituitary size; it was otherwise characterized by carrying recessive genetic factors for myoclonus, and apparently by having a body temperature slightly lower than that of other races.

Factual data concerning body size in the chief races and hybrids used in this study are recorded in the form of percentile analyses.

Median body weight was higher in males than in females of most races. This was not true for Magpies and White Kings, nor for dove races *44* and *N2*. The two last-named races were otherwise characterized as the two dove races which showed greatest intestinal length.

Body weight was highest in dove races *67* and *78*, and lowest in races *N.1* and *6*. The greatest difference in male body weight among dove races was found between races *N.1* and *67*; here the median body weights differed by about 15 per cent of the heavier race (*67*); for the females of these races this difference was 8 per cent. The greatest difference between females was 13 per cent, and this was observed in races *6* and *78*.

Ascariasis affected body weight little and in an inconstant manner in both doves and pigeons; other prevalent diseases produced marked emaciation.

Certain considerations suggest that two mechanisms may operate in the hereditary alteration of body weight, one such mechanism increasing weight in males only and the other increasing or decreasing weight regardless of sex.

The data obtained from the crossing of any two races are insufficient to provide suitable evidence on the number or nature of genetic factors concerned in the inheritance of body weight. The body weight of most hybrid types, among both doves and pigeons, was intermediate to that of the parental races. Heterosis, i.e., increased weight in F_1, was observed in *N2* × *62* hybrids, and perhaps in *72* × *62* hybrids; among pigeons a definite heterotic increase in body size was observed only in females derived from a cross of Tipplers with race *267*.

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3

THE ESTABLISHMENT OF "THYROID" RACES IN DOVES

In the introductory chapter we described the precautions taken to eliminate, or at least to equalize for the several races, the many conditions which are known to cause enlargement of the thyroid glands. In retrospect it is clear that goiter became fairly common in the years following 1930 in most of our races of doves and in practically all our races of pigeons. It should be stated at once, however, that the advent of this tendency to goiter, though it introduces a disturbing factor into the summarization of the present data, did not prevent the accumulation of satisfactory evidence for genetic differences between the various races of ring doves. Indeed, both Bauer[1] and Davenport[2] have insisted that the hereditary factors which permit the development of goiter in man are "best studied where goiter is endemic, provided always that the optimal exogenous factors are not extreme." A point for emphasis, however, is that the data to be presented here are not intended to answer questions concerning the number and nature of the genetic factors regulating thyroid size in doves and pigeons. Primarily the present data were obtained to supply the answer to a single question: From a population of ring doves apparently quite comparable in mongrelization and diversity of thyroids to the human population of an American city, is it possible to establish races with differing size and function of thyroid glands?

Historical

No previous study of the present problem, as this is stated immediately above, has been made in any population. An important part of the present evidence concerning the inheritance of thyroid size in doves was published in 1929, and that paper[3] may be consulted for some instances of behavior of thyroid size in F_1, F_2, F_3, and F_4, and for still other details, which will not be repeated here. Several related questions, however, deserve immediate consideration.

Of course, the establishment of races characterized by differences in thyroid size and functional levels is a possibility only in case these differences are affected, or partly controlled, by genes. The attempts that have been made to identify such genes have been restricted largely to studies relating to the occurrence of goiter in man. Those studies make it practically certain that a gene (or genes) affecting thyroid function exists, though it is also generally agreed that endemic goiter mainly arises as a response to external causes. A brief reference to that literature is necessary.

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[1] Bauer, K. H., Bruns Beiträge zur klin. Chirurgie, 1926, vol. 135, p. 5; 1926, vol. 137, p. 179.

[2] Davenport, C. B., The genetical factor in endemic goiter (Carnegie Inst. Wash. Pub. 428, 1932).

[3] Riddle, O., Amer. Naturalist, 1929, vol. 63, p. 385.

Davenport,[2] from studies on goiter in western Maryland, was led—perhaps erroneously—to the following conclusions concerning genetic factors for goiter susceptibility in man (p. 44):

> This formula is, to recapitulate, that goiter susceptibility depends upon two cooperating factors: one a sex-linked, dominant gene; the other, a dominant, autosomal gene. . . . However, that just two genic factors are always present in goiter cannot be concluded, though this is a minimum number which meets the conditions afforded by the families studied. The distribution of goiter in the families would meet the conditions presented by three or more genes and it would not be surprising if, in some localities in various parts of the world occupied by diverse peoples, the genes permitting goiter enlargement should be different in kind and in number from those we ascribe to the families of Georges Creek Valley.

Quite different conclusions were reached in the more recent study made in Denmark by Bartels.[4] The evidence obtained from this carefully conducted study indicated that both nontoxic goiter and Graves' disease are phenotype manifestations of the same recessive sex-limited gene; and it was assumed that modifiers of this gene exist and are widespread in human populations. Bartels cited and reviewed critically the earlier literature on this subject.

It is of both practical and theoretical importance to know whether thyroid size differs according to sex in material obtained from any animal species. The following statement,[5] written in 1929 before goiter became a disturbing factor in our colony, applies to a large segment of the data obtained in the present study:

> Weights were obtained on the thyroids of 1917 healthy ring doves and on 602 healthy common pigeons aged 4 to 36 months. Within these age limits there is little or no change in body weight, and in many of the 71 races or hybrid types studied there was little or no change in thyroid weight. The large influence of the hereditary factor in thyroid size, and many well-known physiological factors, have here been adequately equalized or controlled; but thyroid weight nevertheless shows itself to be highly variable. Mean values obtained from the union of all comparable races and types of ring doves indicate an excess weight (per unit body weight) in the females of 4.5 per cent (24 races), or of 1.8 per cent (28 kinds of hybrids). This mean for 19 racial and hybrid types of common pigeons is 7.0 per cent. In general, those races which have the *smallest* thyroids show the *smallest percentage sex difference in thyroid size;* in races characterized by *larger* thyroids, the *female glands exceed those of the males by a notably higher percentage.* We interpret these facts as indicating that many individuals of these races have thyroid enlargements similar to those of endemic goiter; and that, as in the human, the females are more often thus affected than are the males.

In view of the above results it was found practicable, in summaries given here, to combine thyroid weights of the two sexes of ring doves (body-weight difference being ignored). For pigeons, however, thyroid weights from the two sexes are given separately.

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[4] Bartels, E. D., Heredity in Graves' disease (Einar Munksgaard, Copenhagen, 1941).

[5] Riddle, O., Amer. Jour. Physiol., 1929, vol. 90, p. 495 (abstract); Endokrinologie, 1929, vol. 5, p. 16.

The results of Hammett's biometrical study on weights of endocrine organs of albino rats (aged 150 days) have some bearing on the question now under discussion. Hammett[6] found that in rats previously maintained at usual levels of thyroid activity, thyroid weight is positively and specifically correlated only with the adrenals. He further found, however, that "the thyroid-adrenal association in the male is less sensitive to general factors of disturbance than it is in the female" (p. 112).

In a study of more than 900 day-old chicks, belonging to six different groups, Aberle and Landauer[7] found that actual and relative thyroid weight was slightly greater in the females. Even at this early stage thyroid variability was quite high, and it was equally high in the two sexes. The authors suggest that the agencies responsible for this variability "are to be looked for in the composition of the eggs from which they hatched as well as in genetic factors affecting thyroid size."

Evidence for a genetic difference controlling susceptibility to enlargement of the thyroid by thyrotrophic hormone was found in 2-day-old White Leghorn chicks obtained from two different sources in Indiana.[8] Chicks from one source required four times as much thyrotrophin to produce a particular amount of thyroid increment as was required in chicks from the other source; and maximal stimulation during a 5-day test yielded thyroids weighing 15 mg. in chicks of the one type and 35 mg. in the other type. Control thyroids weighed approximately 4 mg. in both breeds.

The same authors[8] described a progressive stepwise change in thyroid weight in 862 young White Carneau pigeons procured during a period of 5½ years. The birds utilized in that study were reared until 6 weeks after hatching at the Palmetto Pigeon Plant in Sumter, South Carolina; they were then expressed to this laboratory and examined 7 to 10 days thereafter. During the first 2 years (1936 to 1938) of observation the average weight of the thyroids of such birds was close to 40 mg. A stepwise increase in thyroid weight occurred in the autumns of 1938, 1939, and 1940 without complete return to previous summer levels; early in 1941 an average weight of 179 mg. was attained. The cause of these changes is largely unknown; but change of source of food and grit, and unrecognized infection may be suspected.

McCarrison[9] concluded from his studies that ingestion of fecal matter is highly goitrogenic in pigeons, probably through change in the bacterial flora of the intestinal tract. He further showed that inclusion in the diet of certain foodstuffs, such as fats, tends to produce goiter when the iodine supply is at or near the minimum.

[6] Hammett, F. S., Jour. Metab. Res., 1926, vol. 8, p. 91.

[7] Aberle, S. D., and W. Landauer, Anat. Rec., 1935, vol. 62, p. 331.

[8] Bates, R. W., O. Riddle, and E. L. Lahr, Endocrinology, 1941, vol. 29, p. 492.

[9] McCarrison, R., Indian Jour. Med. Res., 1919, vol. 6, p. 275; 1923, vol. 11, p. 1; The simple goitres (Baillière, Tindall & Cox, London, and W. Wood, New York, 1928).

Landauer and Aberle[10] found that the thyroids of Frizzle chickens are heavier (at the age of 8 months) than those of White Leghorns. The basal heat production was also much higher in the Frizzles.[11] In both of these respects Frizzle fowl resemble the scraggly pigeons utilized in the present study. Also, the basis for these differences is to be found in the defective plumage of these birds; neither frizzled nor scraggly feathers provide the usual protection against loss of body heat.

Secondary to our chief aim—that is, to learn the possibilities of establishing races with endocrine structures and functions genetically fixed at different levels —was the relatively simple task of learning something of the extent to which this kind of endocrine difference had unintentionally been attained in some of the many varieties of fancy or domestic pigeons. Our material, like the various breeds of dogs used by Stockard, often included types showing wide differences in size, in conformation of body and head, in reproductive and other capacities, and in temperament. Determination of size and the functional level of the thyroids in some of these well defined breeds—all in connection with the other measurements made in the present study—seemed to offer information of value concerning these divergent races. In such a study it was essential that these several breeds be given the same diet and otherwise reared under identical living conditions. In the pursuit of both our primary and secondary aims, thyroid size was determined by weighing the glands from freshly exsanguinated animals; and level of thyroid functioning was determined by measurement of the basal metabolic rate (see part II).

The results obtained by Stockard and Vicari[12] on the thyroids of different breeds of dogs are to be noted here. In terms of milligrams of thyroid weight per kilogram of body weight, the thyroids of Basset hounds and Dachshunds were much larger than those of Great Danes and St. Bernards. The variation observed among apparently healthy individuals of a breed was always considerable, and for some breeds it was extreme. For example, in 13 adult English bulldogs thyroid sizes ranged from 55 to 305 mg. per kilogram of body weight. Usually only a few thyroids were available for each race. As an index of thyroid function Stockard and Vicari utilized histology of the thyroids, and from histological study they concluded that in certain breeds there is an apparent correlation between the histological structure of the thyroid and the physical type (skull distortion) of the animal. No causal relation was affirmed in these cases because of various possibilities, including the possibility that the pituitary gland caused both the thyroid modification and the skull distortion. Pursuit of this problem by Stockard and Vicari therefore included studies on the size and histology of the pituitary glands of certain races and hybrids. There also, in certain cases, the histological patterns of the pituitaries were observed to show differences more or

[10] Landauer, W., and S. D. Aberle, Amer. Jour. Anat., 1935, vol. 57, p. 99.

[11] Benedict, F. G., W. Landauer, and E. L. Fox, Storrs Agric. Exper. Sta. Bull. 177, 1935.

[12] Stockard, C. R., and E. M. Vicari, sec. V *in* Stockard, C. R., The genetic and endocrinic basis for differences in form and behavior (Amer. Anat. Mem., no. 19: Wistar Inst., Philadelphia, 1941).

less closely associated with certain differences in morphological type. It would appear that, in the opinion of these investigators, pituitary differences provided a better basis for the morphological differences than did thyroid differences, but a clear statement on this point was apparently not made.

Brown[13] discussed constitutional variation in its relation to susceptibility to disease; the anatomical data which he considered were obtained from a single breed of rabbits. Brown and associates observed that in 645 normal rabbits, weight of the thyroid increased in winter and early spring and decreased in late spring and early summer; in midsummer there was again a marked increase, and this was followed by an equally marked decrease in the autumn. On the other hand, the weight of the pituitary increased only once annually, slightly before the summer increase in thyroid weight.

Wild Norway rats were observed by Donaldson and King[14] to have lighter pituitaries and heavier adrenals than Wistar albino rats, but practically equal thyroid weights. Wistar rats were reported to have lighter thyroids and adrenals, but heavier pituitaries, than rats of the Long-Evans strain.[15] Two studies have been made on thyroid size in rats selected and bred on the basis of their degree of emotional or nonemotional response. In one of these studies[16] the two psychological types showed a difference in the pituitary, but not in the thyroids or adrenals. In the other study[17] male emotional rats had heavier thyroids and adrenals, but their pituitary weights did not differ from those in the other type; emotional female rats, however, had significantly heavier thyroids and pituitaries, but not heavier adrenals, than nonemotional females. The authors of this latter study rightly noted that a causal relation is not proved here, since the emotional rats may, independently of their emotional response, have acquired a tendency to goiter.

ANATOMICAL AND GENERAL

The two wholly independent thyroids of doves and pigeons are located at the anterior border of the thoracic cavity, 2 to 3 cm. from the heart and apposed to the jugular vein and the carotid artery. Typically, they are of the shape and size of a grain of rice, and their exposed firm surfaces permit them to be separated cleanly from all extraneous tissue and weighed with quite satisfactory accuracy. All thyroids were preserved in formalin; this was to permit later histological study if it should prove desirable. Relatively few glands were thus examined, and the results were not particularly significant. Seasonal changes, and unclear indications of change in thyroids of females at or near ovulation, were observed; but detailed study such as would be required to differentiate the various races was not attempted. Indeed, this seemed unnecessary since functional levels of the thyroids of these groups were determined after 1927 by measurements of the basal heat production.

---

[13] Brown, W. H., Arch. Internal Med., 1929, vol. 44, p. 625.

[14] King, H. D., and H. H. Donaldson, Life processes and size of the body and organs of the gray Norwegian rat (Amer. Anat. Mem., no. 14: Wistar Inst., Philadelphia, 1929).

[15] Freudenberger, C. B., Amer. Jour. Anat., 1932, vol. 50, p. 293.

[16] Anderson, E. E., and S. F. Anderson, Jour. Comp. Psychol., 1938, vol. 26, p. 459.

[17] Yeakel, E. H., and R. P. Rhoades, Endocrinology, 1941, vol. 28, p. 337.

It seems well to record certain abnormalities of thyroids which have been observed either in the present material or in the large number of younger birds (under 4.0 months) which have been used in related studies during the past 25 years. Two pairs (instead of one) of thyroids, 1 to 2 cm. apart, were found twice: once in a pigeon (*SA-R*) and once in a dove hybrid (*NE* × *63*). In one dove (race *67*) the two thyroids were displaced anteriorly to the extent of 2.0 and 3.3 cm. In one dove (*NA* × *72*) the two thyroids were each in the form of a string, 28 to 31 mm. long, and little more than 1 mm. in width. In two doves (*75* × *B*; *72* × *206*) the left thyroid was absent. The right thyroid was absent in two pigeons and three doves (*63*, *67*, *65* × *63*). Krause[18] stated that accessory thyroid tissue is always to be found in the sublingual region of pigeons. Observations made in this laboratory suggest that no more than microscopic amounts (if any) of such tissue exist in most of the birds of our colony. In a few pigeons which had been thyroidectomized several months earlier, however, these "rests" were readily found; since such accessories were larger than any observed in unoperated birds, it is obvious that they increased in size following thyroid removal.

It was shown by Riddle and Fisher[19] that the thyroids of doves and pigeons aged 30 to 90 months are usually noticeably larger than those of younger birds of the same race. From the following tabulations all data from pigeons aged more than 4 years are excluded; no dove thyroids were excluded on the basis of age alone, but very few glands were obtained from doves older than 4 or 5 years.

The relative rarity of really large thyroids in doves is notable. A total of only 41 pairs of glands were found to have a weight of more than 100 mg.; these included 29 from dead or diseased birds. The sexes were about equally represented. Only 10 of the 41 pairs of glands weighed more than 150 mg., and only 2 weighed more than 300 mg. The larger of these 2 weighed 985 mg., the smaller 306 mg. Among pigeons, however, glands of extreme size—up to 14 gm.—were sometimes observed. The various pigeon races showed great differences in the frequency and extent of goitrous development. For example, among birds autopsied during 1940, only 1 of 49 individuals of the "hermaphrodite-producing race" (*T* × *267*) had a pair of thyroids weighing more than 200 mg.; but 13 of 43 Carneaux had such glands, some of which weighed more than 1.0 gm.

Thyroid Size in Dove Races and Hybrids

The data on thyroid size in doves are presented in figures 31 to 63. As earlier noted (see "Statistical Procedures" in chapter 1), the principle of "moving medians" is used to smooth the curves. In all cases, the values given for hybrids include all (F_1, F_2, and F_+) generations. The justification for this procedure is perhaps adequately indicated by the data of figure 57; these generations (unusually large populations) are there plotted separately.

[18] Krause, R., Mikroskopische Anatomie der Wirbeltiere in Einzeldarstellungen, pt. 2, 1921 (W. de Gruyter & Co., Berlin and Leipzig).

[19] Riddle, O., and W. S. Fisher, Amer. Jour. Physiol., 1925, vol. 72, p. 464.

FIG. 31

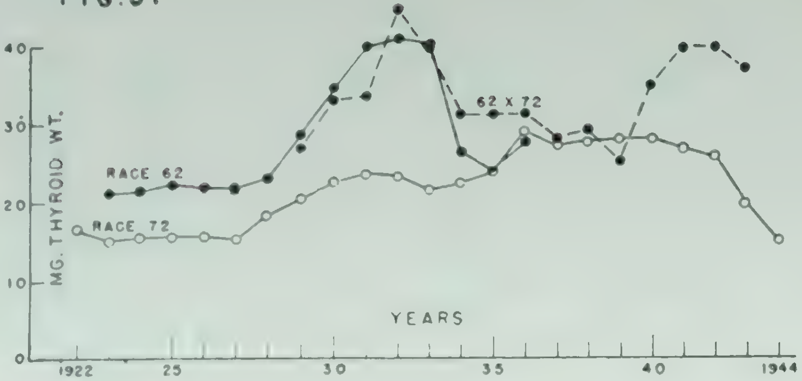


FIG. 32

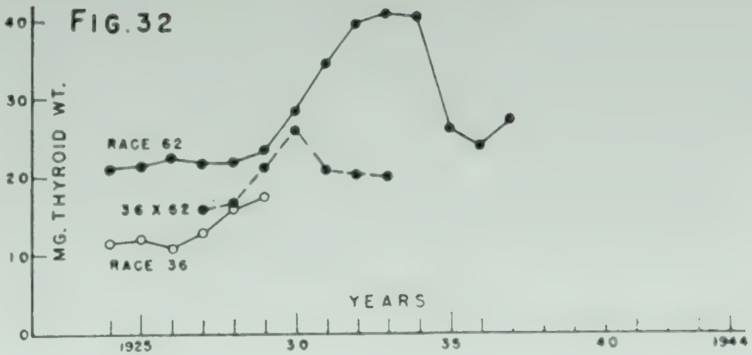


FIG. 33

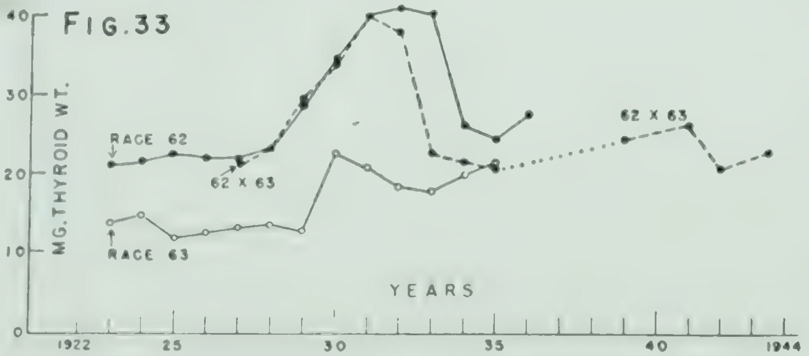


FIG. 34

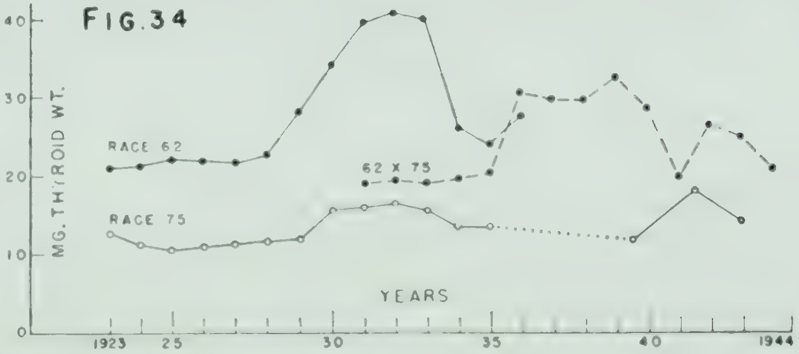


FIG. 35

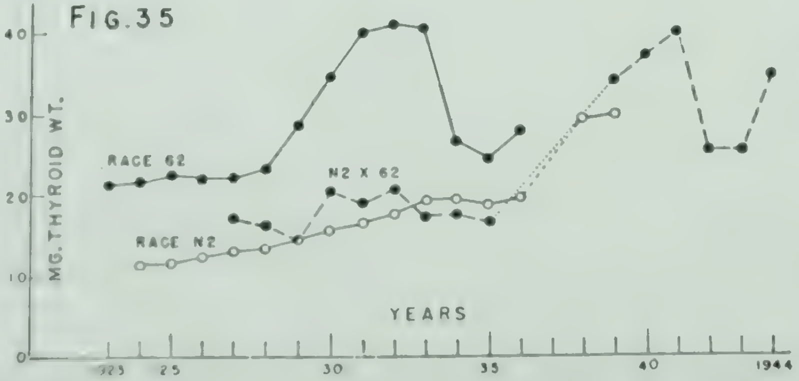


FIG. 36

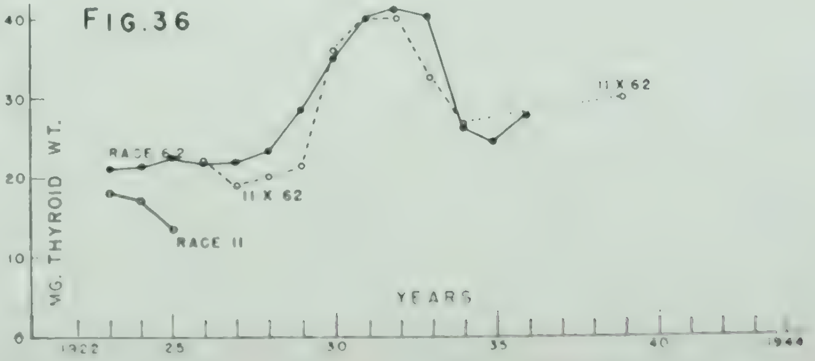


FIG. 37

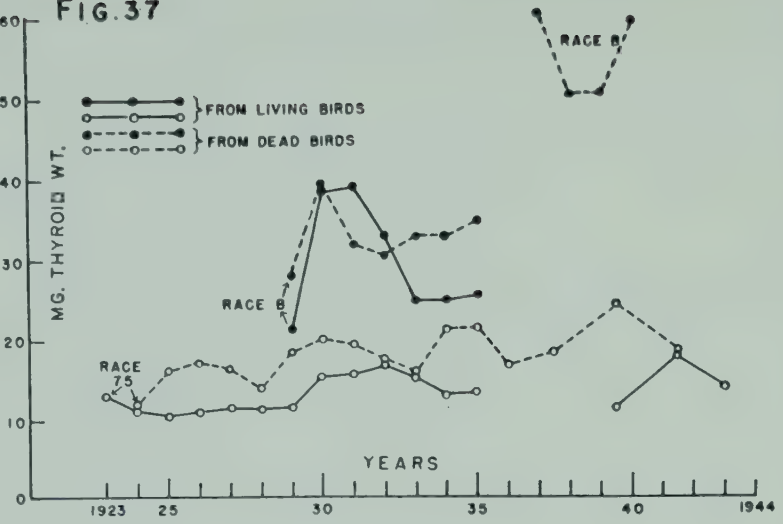


FIG. 38

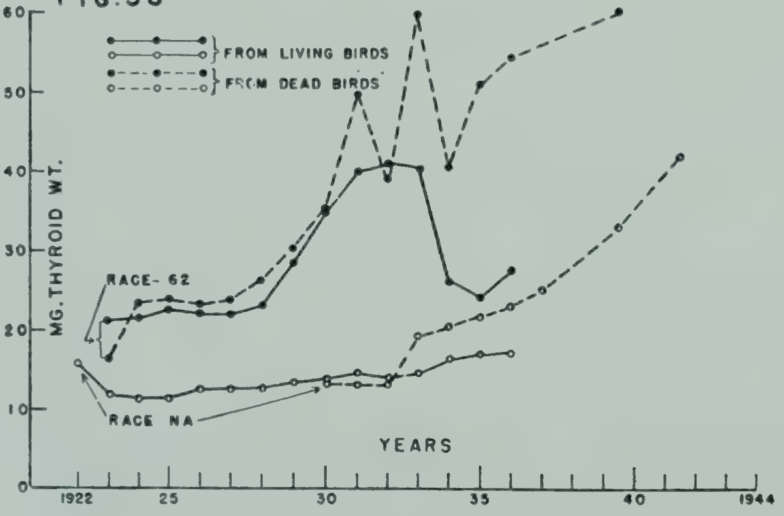


FIG. 39

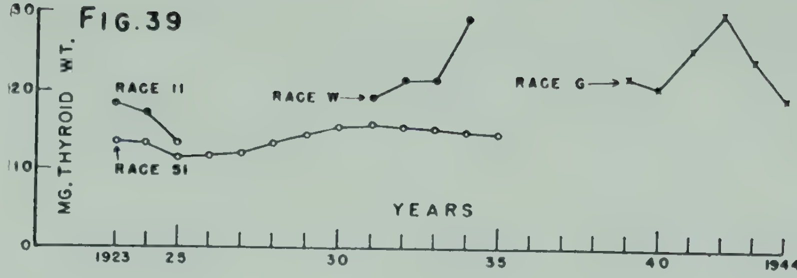


FIG. 40

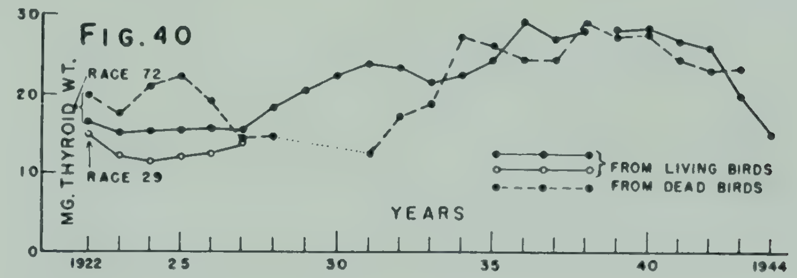


FIG. 41

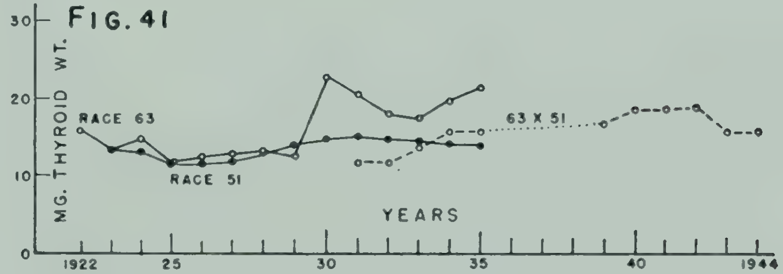


FIG. 42

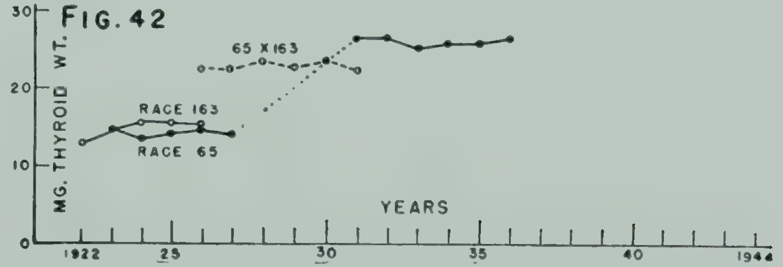


FIG. 43

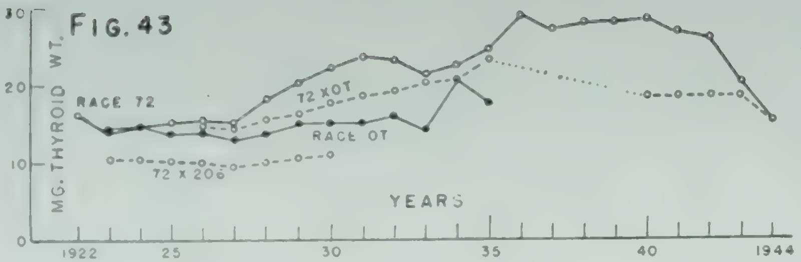


FIG. 44

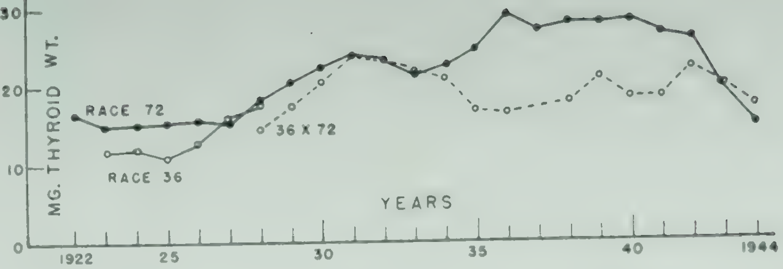


FIG. 45

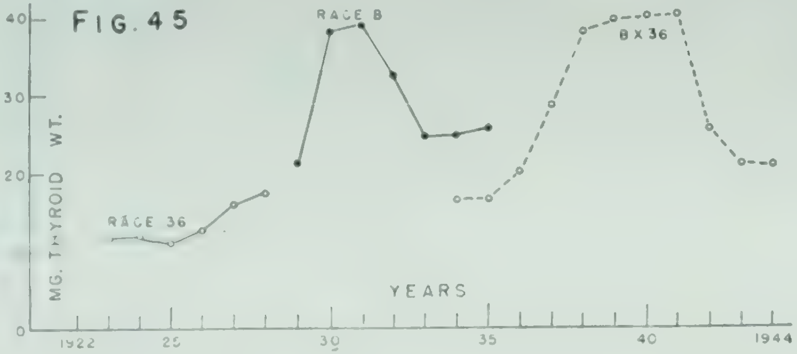


FIG. 46

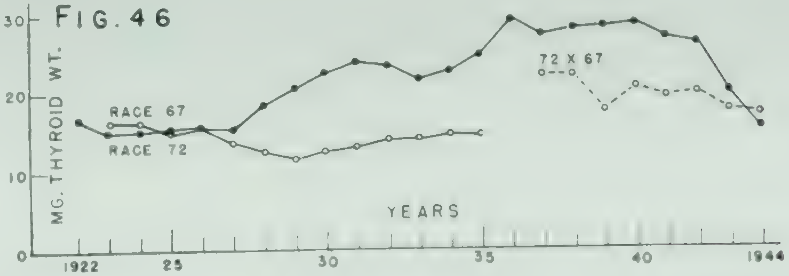


FIG. 47

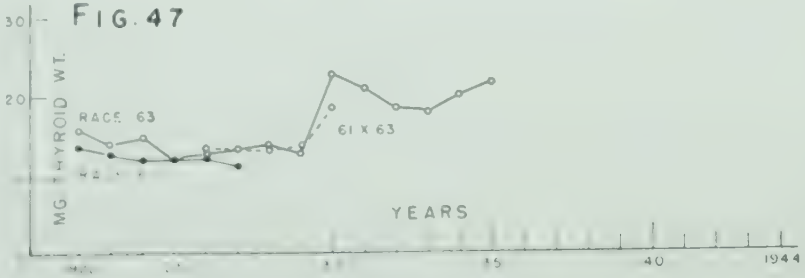


FIG. 48

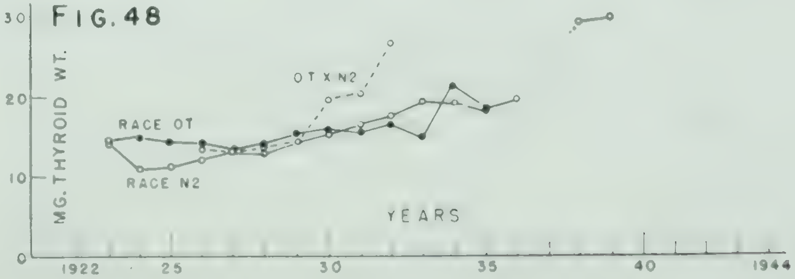


FIG. 49

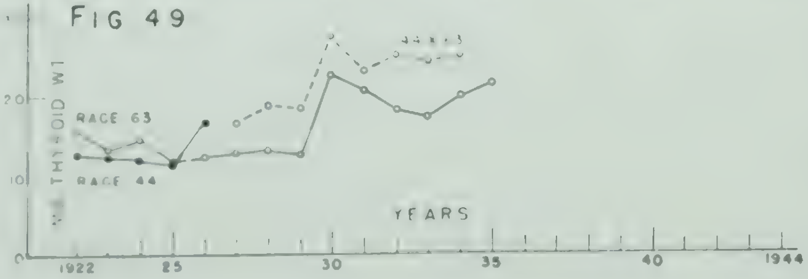


FIG. 50

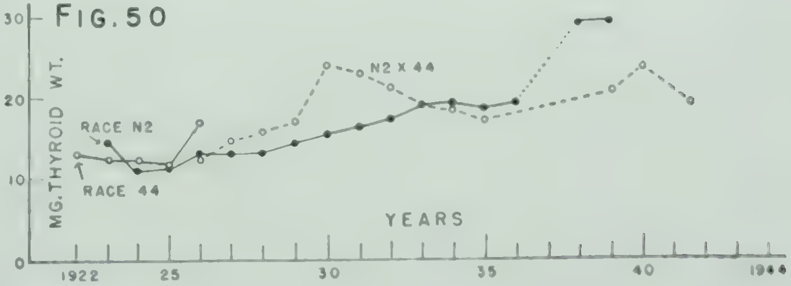


FIG. 51

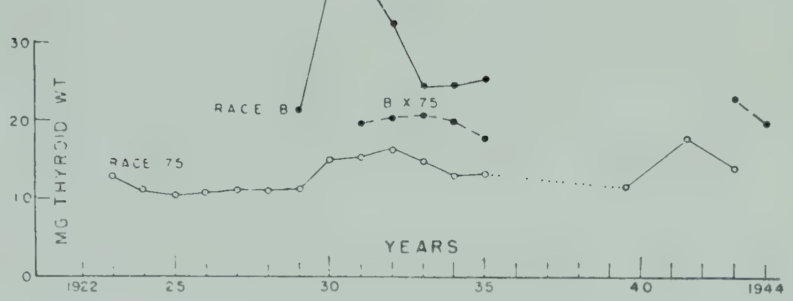


FIG. 52

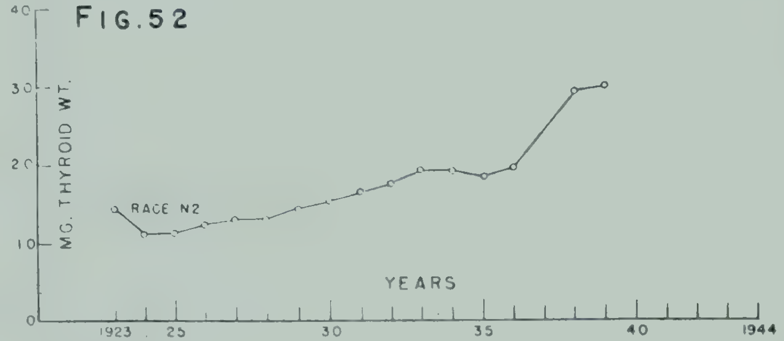


FIG. 53

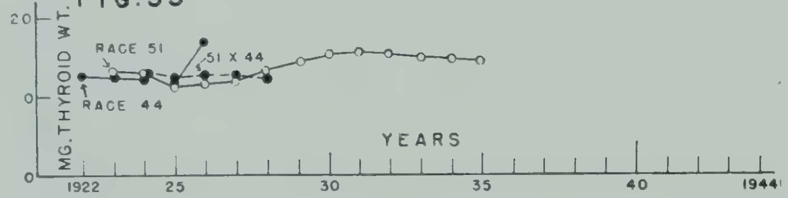


FIG. 54

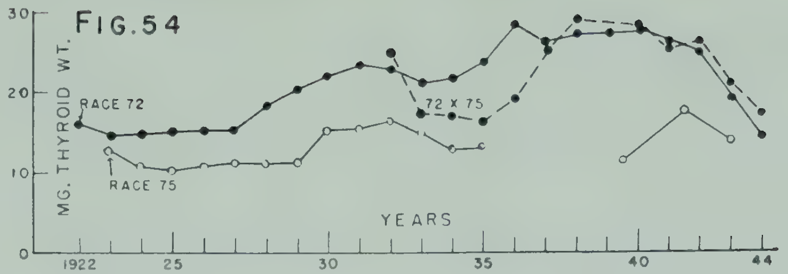


FIG. 55

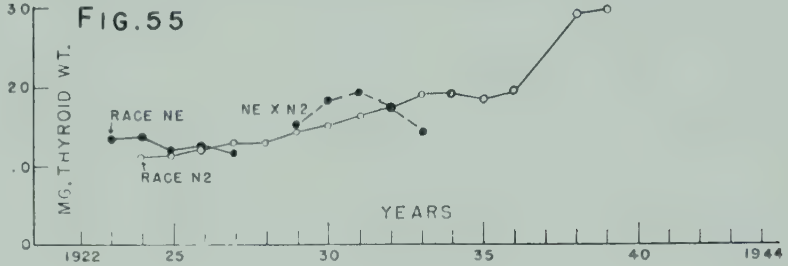
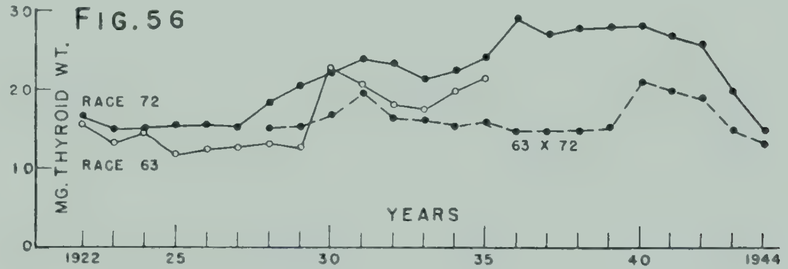


FIG. 56



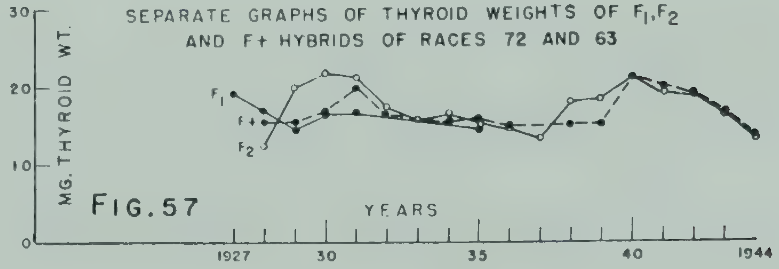


FIG. 57

FIG. 57. F1, F2, and F+ generations obtained from crossing races 72 and 63 are plotted separately. Compare these values with the single curve formed from their union in figure 56, immediately above.

FIG. 58

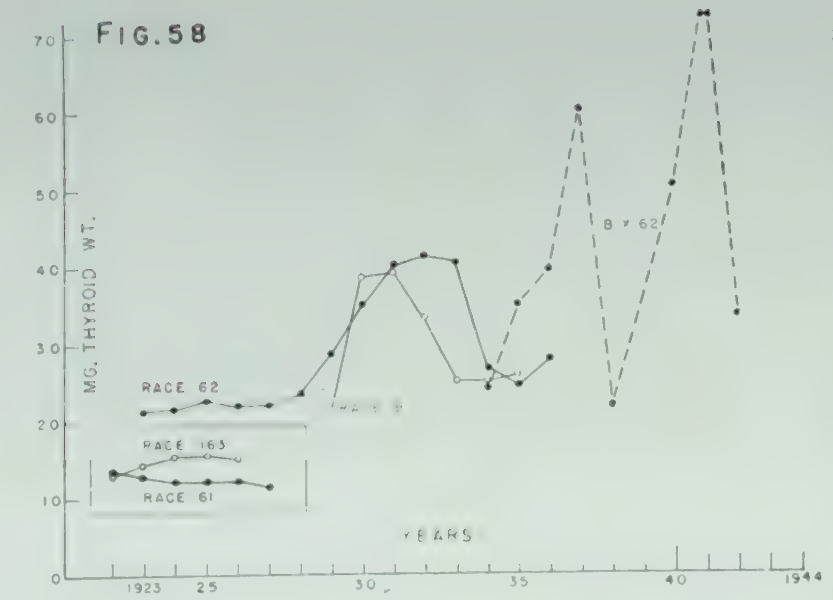


FIG. 59

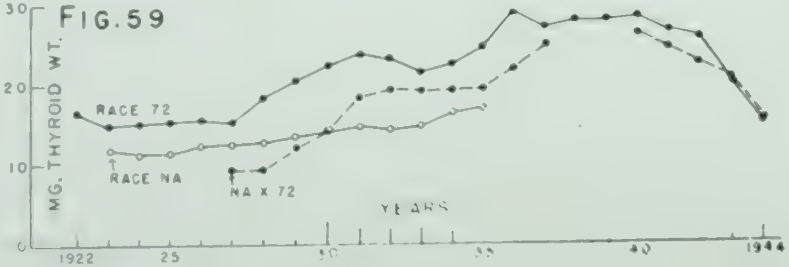


FIG. 60

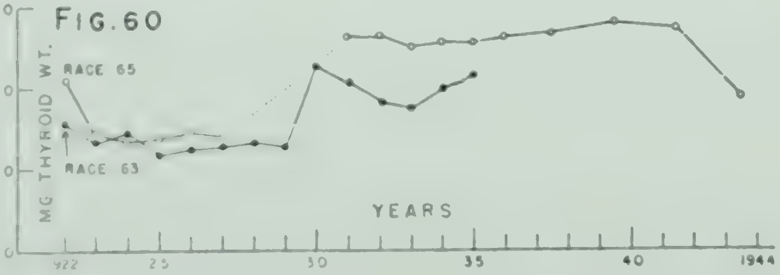


FIG. 61

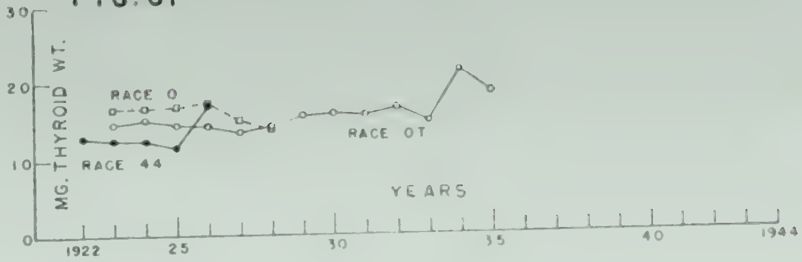


FIG. 62

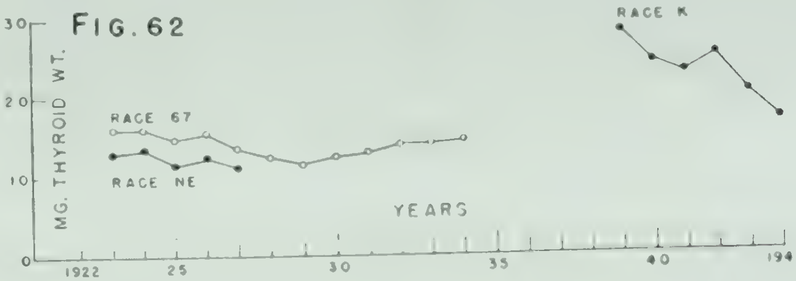
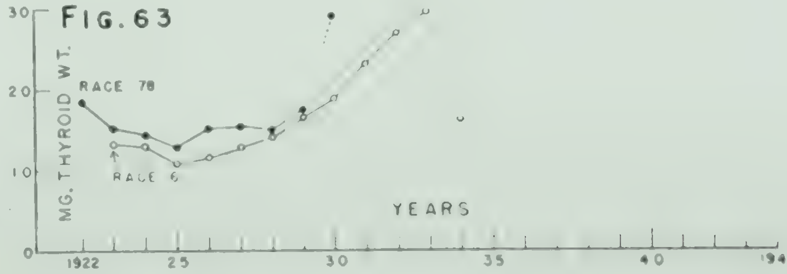


FIG. 63



A general survey of the present data indicates that although the thyroids of most groups tended to enlarge after 1930, this tendency was little if at all evident in the case of races *67* and *51* and in *72* × *63* hybrids. In general, only thyroids from apparently healthy birds are used in the construction of the curves, but it is to be noted that glands from dead and diseased birds were actually (see below) not markedly larger than those from healthy birds. Separate curves have been constructed for the two types of birds of 5 races (figs. 37, 38, 40). In these cases it is evident that the genetic differences which regulate thyroid weight are indicated almost as well (except perhaps in race *75*) by data from the dead and diseased as from healthy doves. The somewhat larger thyroids of the dead birds, indicated on the curves, may be largely due to the fact that the dead birds were not exsanguinated and their glands therefore contained an excess of blood.

Since differences in body weight of the various races are slight, the summarizations given in the several curves demonstrate that the thyroids of these races were genetically held at various levels, high, low, or intermediate. Attention will be directed to the more significant cases. In figure 51 it is shown that thyroids were large in race *B* and small in race *75* (selected); hybrids from these races were definitely of intermediate size. Figures 50 and 53 show that races *51*, *N2*, and *44* all had thyroids of small or intermediate size; also that hybrids produced by crossing race *51* or *N2* with race *44* (soon lost) had thyroids similar to those of the parent races. These conditions are repeated in the case of races *NE* and *N2* and their hybrids (fig. 55). Race *72* (selected) had fairly large thyroids, and in crosses with the low-thyroid race *75* the hybrids (fig. 54) were either intermediate or nearer to race *72*. When race *72* was crossed with low-thyroid race *NA* the hybrids at first tended to have thyroids smaller than those of *NA*, but following 1930 the thyroids of the hybrids were definitely of intermediate size. In figure 43 it will be observed that extremely small thyroids were obtained from *72* × *206* hybrids. It should be stated that the individual of race *72* used in this test was a first-generation (unselected) male whose thyroids proved to be surprisingly small (11.2 mg.). In crosses of race *72* with race *63* (intermediate thyroids) the thyroids of hybrids were at first of intermediate size, but following 1930 they seem to have been less affected by goitrogenic agents than those of either parent race (fig. 56). When race *72* was crossed with a race with extremely large thyroids (race *62*, selected), the hybrids (fig. 31) tended to have thyroids equaling or exceeding those of race *62*.

Five additional crosses of race *62* gave particularly informative results. In its crosses with (intermediate) race *63* the thyroids of the hybrids were either intermediate to those of the parent races or equal to those of race *62* (fig. 33). Crosses of race *62* with three low-thyroid races (*N2*, *36*, and *75*) produced hybrids whose thyroids tended to be intermediate to those of the parental races (figs. 35, 32, 34). When race *62* was crossed with the other race (*B*) which was likewise characterized by extremely large thyroids, the glands of the hybrids were like those of the two parental races; and during the years when goitrogenic conditions were most prevalent these hybrids were characterized by much larger thyroids than were obtained from any other population of doves in the colony (fig. 58).

Extremely small thyroids were obtained from race *61* (selected); this race was lost early (fig. 58). Other races characterized by small thyroids are *75*, *44*, *NE*, *29*, *NA*, *51*, and perhaps *36*, *6*, and *N2*. Race *11* (selected; fig. 39) was lost early (as were closely related doves known as *11a*), and progress was not made in establishing large thyroids in the race itself; however, birds of these groups (*11* and *11a*) when used in crosses yielded hybrid groups (also lost early) with average thyroid weights ranging from 15.6 to 27.1 mg.[20] The thyroids of race *65* (selected; fig. 42) were maintained only slightly above those of an intermediate race (*63*). Other races characterized by large thyroids were *62*, *B*, and *72*. Races with thyroids of intermediate size included *63*, *163*, *67*, *O*, *OT*, and *78* (?*6* and *N2*). Three supplementary groups (*G*, *W*, and *K*; figs. 39, 62) apparently had thyroids of larger or of intermediate size, but their thyroids were weighed only or mainly during a period when thyroid enlargement was prevalent.

Thyroid-Liver Relations in Ring Doves

It was noted above that thyroid weights from doves that died (not exsanguinated) are only moderately heavier than those from healthy (exsanguinated) doves. In chapter 6 it is shown that the median weights of livers from dead (not exsanguinated) doves and pigeons are much greater than those from healthy birds. Figures 64 and 65 provide a summary (percentile analysis of representative parts of our data) of thyroid-liver relations in the two health groups of both sexes. It may be recalled that liver size is 10 to 12 per cent greater in females than in males. For random groupings in which race is disregarded, the data of figure 64 show that smallest thyroid size is associated with lowest liver weight; heaviest thyroids are associated with greatest liver weights. These data also indicate slightly heavier thyroids in females than in males.

In figure 65 representative data from dove hybrids are presented in a form which differs from that used above. Here percentile analyses are given for the livers, and thyroids of three selected sizes determine the populations represented in the graph. In this case the (healthy) livers associated with thyroids weighing less than 12 mg. weigh only a little less than do livers associated with the two classes of thyroids weighing much more. Again, in the population characterized by thyroid weights under 12 mg. the livers of females are not heavier than those of males.

The data of the two summaries just reviewed do not indicate a really simple relation between thyroid size (and function) and liver size. The existence of a relation, however, is evident. The usual influence of sex on liver size is perhaps not present in doves whose thyroids are quite small; other data (see table 3) indicate that such small thyroids are probably highly efficient.

Thyroid Weight in Pigeon Breeds and Hybrids

A survey graph (fig. 66) provides a view of thyroid size in relation to body weight in 11 breeds of pigeons. Dead or diseased birds are not included in these

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[20] Riddle, O., Amer. Naturalist, 1929, vol. 63, p. 385.

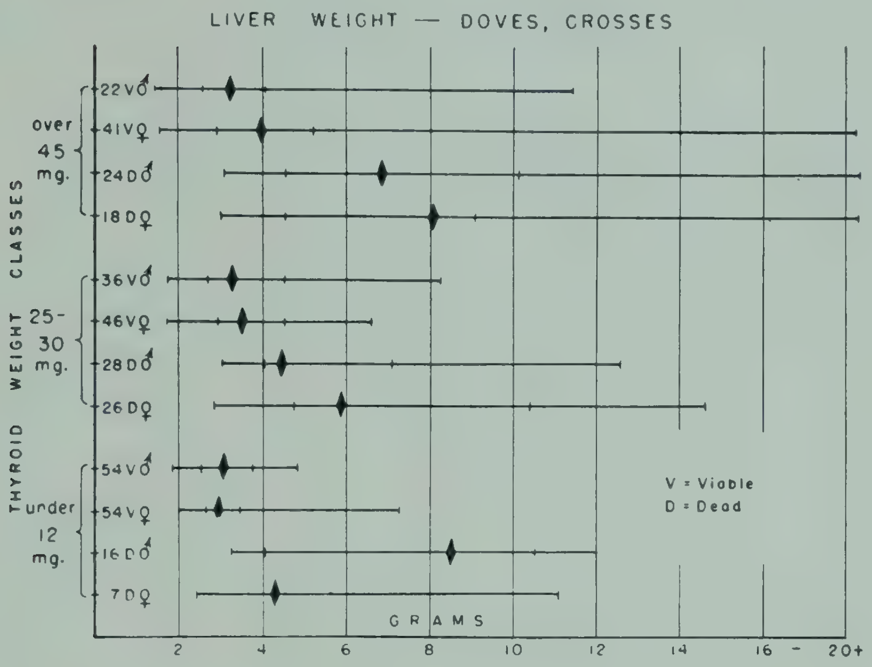

FIG. 64. Three classes of liver weights are shown to be directly associated with corresponding weights of thyroids. In these groupings the thyroid weights of females slightly exceed those of males.

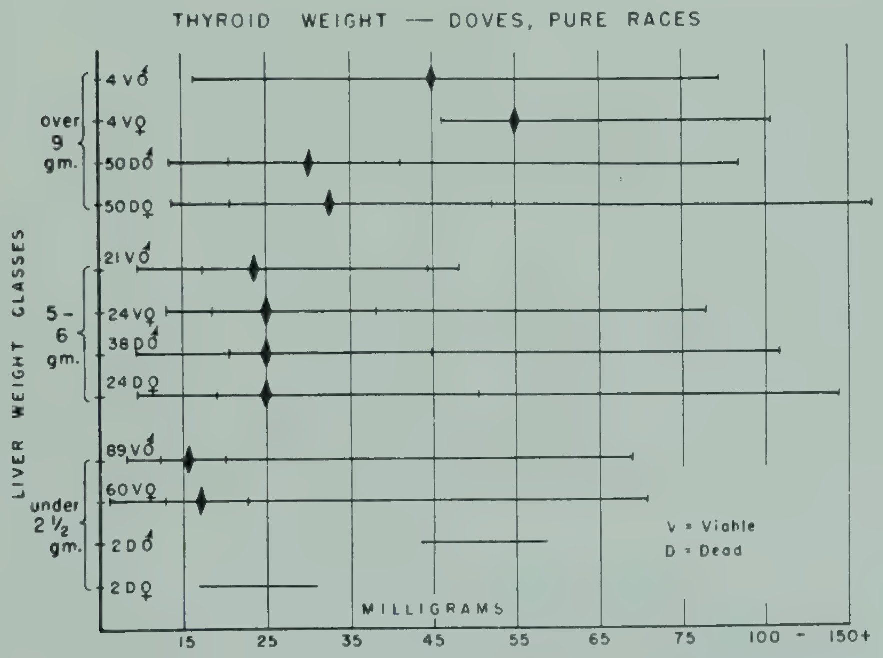

FIG. 65. For these classes of thyroids, two of which represent extremes, the associated liver weights are shown. In this case liver weight varies but little in the three classes.

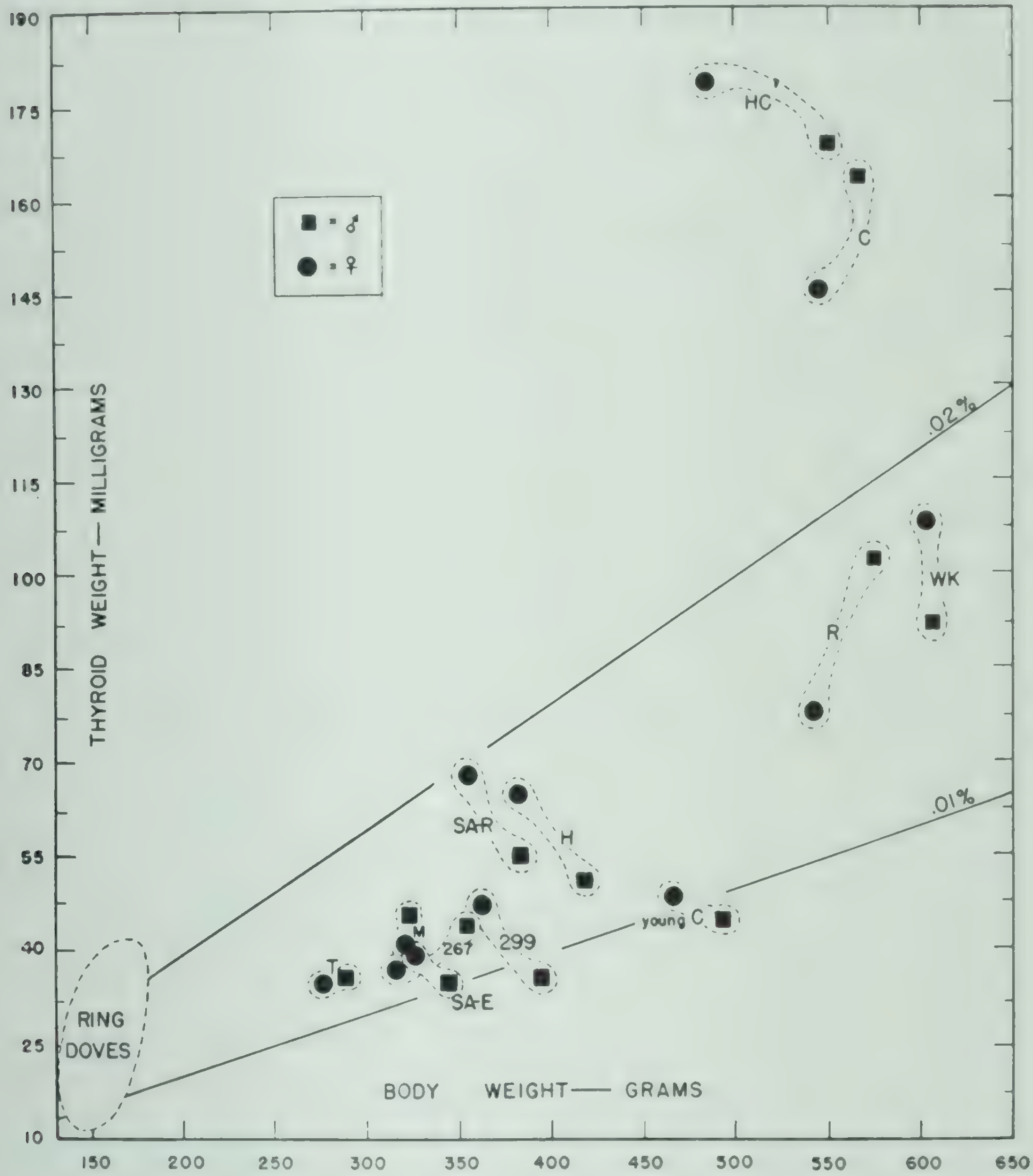

Fig. 66. Survey graph on thyroid weight and body weight of both sexes in 11 races of pigeons. Several races are indicated by initials only (Tipplers, Magpies, Homers, Runts, White Kings, Carneaux, and Homers *C*). Data for "young *C*" (young Carneaux) are not comparable with any other data of the graph (see text).

summaries. The numbers of birds of each sex involved in these measurements may be obtained from the graphs presented in this chapter. Races *299*, *SA-E* (normal type only), and Tipplers seem to have relatively small thyroids; Homers *C* (*HC*) and Carneaux (*C*) apparently have extremely large thyroids. These apparent differences, however, can be partly accounted for apart from a genetic influence. Most of our data for races *299* and *SA-E* were obtained before the time (about 1930) when goitrogenic differences became more evident in our colony; most data for Homers *C* and Carneaux were obtained after 1930. Runts (*R*), however, were reared largely in the earlier periods, and their thyroids were relatively larger than those of most races reared at that time. Again, Tipplers and Homers were reared during both earlier and later periods, but they did not become as goitrous as did Homers *C* and Carneaux. The available evidence indicates therefore that the 4 large breeds studied by us—Runts, White Kings, Homers *C*, and Carneaux—all differ from Tipplers, Homers, and Magpies in one or more genetic factors which permit development of goiter.

The graph indicates that young Carneau pigeons have quite small thyroids. This is probably the true condition for this breed when optimal conditions are provided. The data used for this graph, however, were selected (for the years 1936 and 1937), and data obtained during 1939 and 1940 would indicate much heavier thyroids; moreover, as noted earlier in this chapter, the young Carneaux which showed this stepwise increase in thyroid weights were not reared in our own colony. The graph further indicates that, among the different breeds, sex bears no consistent relation to thyroid weight. As noted earlier, however, measurements made on large numbers of these pigeons before the onset of pronounced goiter indicated[21] that, in terms of percentage of body weight, the thyroids of female pigeons are slightly (7 per cent) heavier than those of males, and this may mean that slightly goitrogenic influences more often affect the thyroids of females.

Percentile analyses of thyroid weight in 10 pigeon races are given in figures 67 to 70. In order to conserve space, initials only are used for such races as Runts (*R*), White Kings (*WK*), Carneaux (*C*), and Tipplers (*T*). In the case of 4 heavy breeds (*R*, *WK*, *C*, and *HC*) the frequency of goiter is so great that the line analyses are quite inadequate; even in those cases, however, relative thyroid weight of the breeds, and of the sexes within each breed, is made evident. In practically all races of pigeons median thyroid weight in dead birds tended to be less than in healthy birds. Parasitization with *Ascaridia*, however, was usually accompanied by increased weight of thyroids; this increase was about 5 per cent in Runts, 15 per cent in Tipplers, and 40 per cent in race *267*, and other races showed increases intermediate to these values. This parasitization is also elsewhere shown to be associated with increased weight in the liver. In terms of percentage body weight, thyroid size was usually greater in females than in males, but Runts, Magpies, and *267* are exceptions.

Races *299*, normal-type *SA-E*, and Tipplers all had small thyroid weights (medians); in terms of percentage body weight, the median (sexes combined, and healthy only) values in these races were 0.0103, 0.0103, and 0.0120, respectively. For races with very large thyroids, the corresponding values were: Homers *C*, 0.0253; Carneaux, 0.0238. Differences in thyroid weights of the three types (normal, scraggly, ataxic) of *SA-E* pigeons are of rather special interest since each of the aberrant types appears to differ from normal by only a single recessive genetic factor. For these types the values, calculated as above, are: normal, 0.0103; scraggly, 0.0136; ataxic, 0.0112. Apparently the scraggly con-

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[21] Riddle, O., Endokrinologie, 1929, vol. 5, p. 241.

FIG. 67

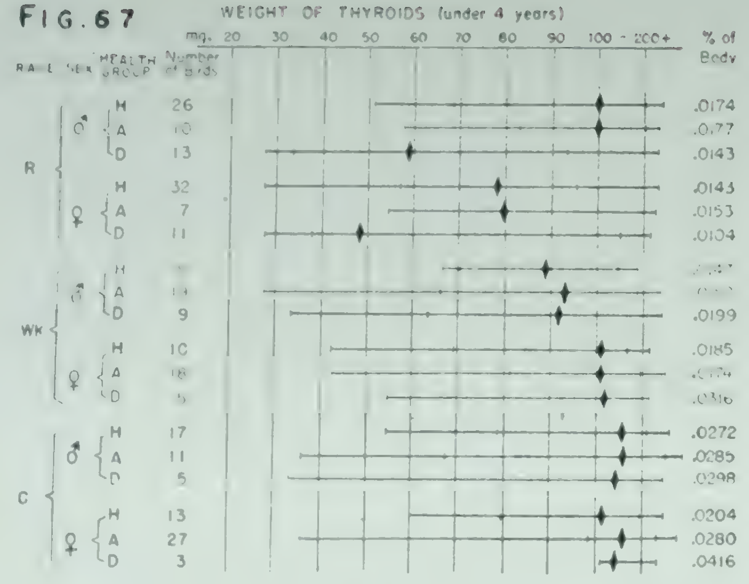


FIG. 68

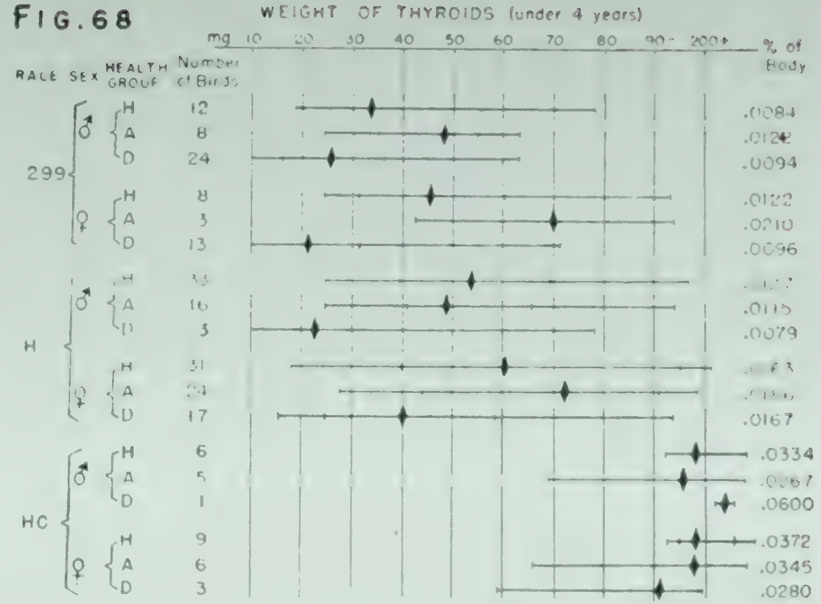


FIG. 69

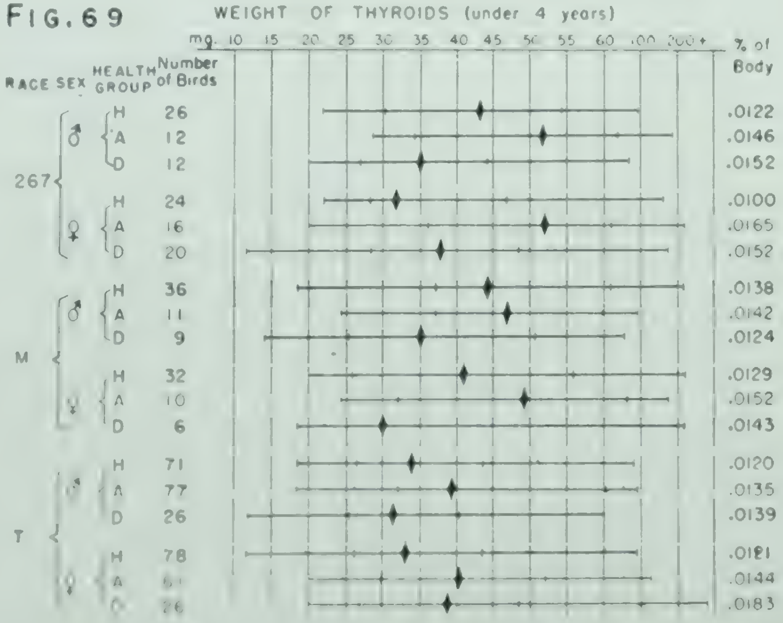
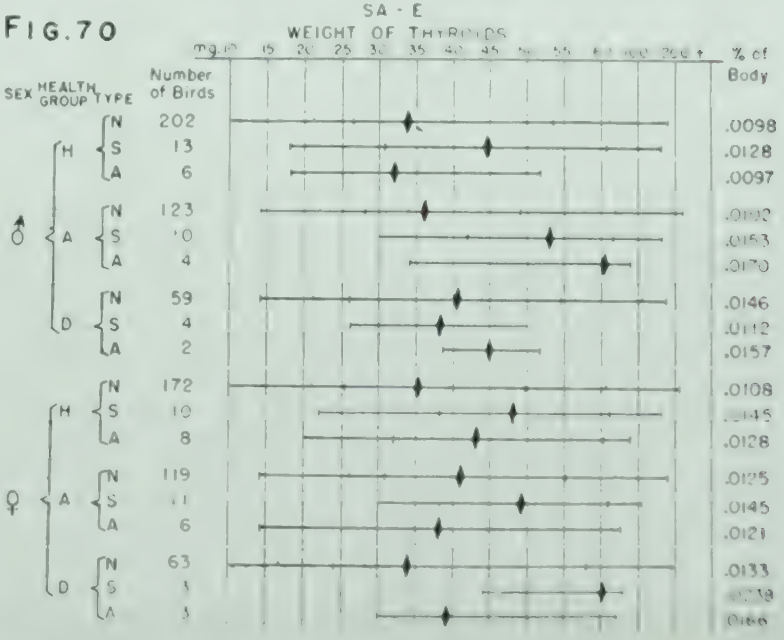


FIG. 70



dition was here associated with a small increase in thyroid size. This was not the case, however, in scragglies obtained from the related race (*SA-R*) which was bred during later years. Details of data for race *SA-R* are not given, but values comparable to those just given for race *SA-E* are as follows: normal, 0.0162; scraggly, 0.0154; ataxic, 0.0166.

In view of the marked goitrogenic (environmental) effects observed in several of the pure breeds during later years of these tests, it is not surprising that the thyroids of pigeon hybrids usually show little evidence of genetic control. It is only, or chiefly, in a very general way that the genetic influence is apparent in the thyroid weights of most of the hybrids. Further unsatisfactory aspects of these data involve the fact that the number of hybrids obtained from some crosses is small, and also the fact that usually the F_+ generations were reared later and under conditions apparently more goitrogenic than those prevalent during the rearing of F_1 and F_2 generations. Nevertheless, it has seemed useful to present percentile analyses of the 9 types of hybrids for which largest numbers of individuals are available.

Data for healthy pigeon hybrids are presented in figures 71 to 79. Graphic devices or lines are used at the top of each analysis to indicate median values obtained for each sex (males above, females below) of each parent race: a *solid* half-diamond pointer indicates the median obtained from healthy birds, and an *open* half-diamond marks the median obtained from parental birds with ascariasis. With the aid of these devices it is easy to determine the relation which the several values obtained from hybrids bear to the median values for the parental races. It is especially notable that F_1 hybrids from Runt and Magpie (fig. 78) had thyroids smaller than those of either parent; but F_1 from Runt and *299* (fig. 75) tended to have thyroids equal to the large thyroids of Runts. These results may be associated with the fact that Runt and Magpie were quite dissimilar and unrelated breeds, whereas race *299* was partly derived from Runt stock.

BRIEF SUMMARY OF RELATION OF THYROID SIZE TO FUNCTIONAL ACTIVITY (HEAT PRODUCTION)

Though the data concerning this subject are given in part II of this volume, it is necessary to note here that measurements of heat production provide essential information concerning the functional levels of the thyroids of the races and hybrids described in the present chapter. Table 3 presents an important aspect of that information in summary form. Some dove races are not represented in this table, except in hybrids. This resulted from the fact that measurements of heat production were not started until 1928, and after that date some races were represented by too few individuals to permit a satisfactory measurement of the race. The measurements actually made on this group of races and hybrids are brought together under the heading "miscellaneous." Chapter 13 may be consulted for additional data concerning the several tabulated values; some heat-production values (obtained at 30° C.) for the several pigeon races are given in terms of surface area in chapter 12 (table 13).

FIG. 71 WEIGHTS OF THYROIDS, MAGPIE X TIPPLER (under 4 years)

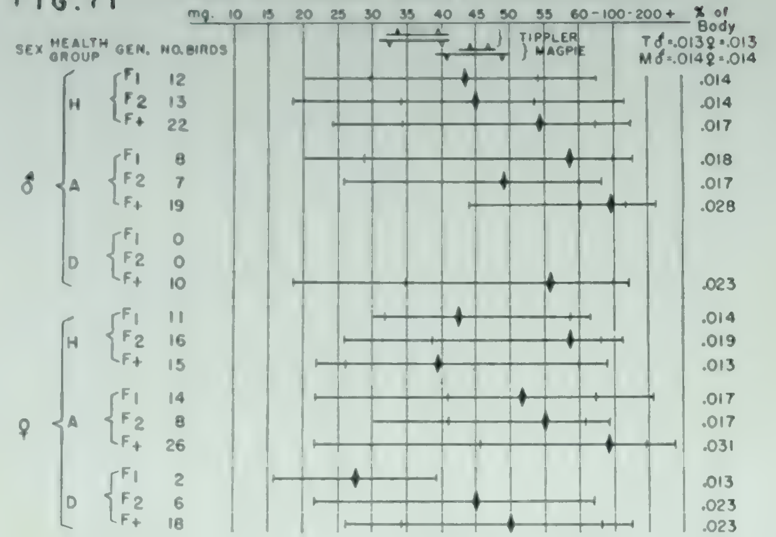


FIG. 72 TIPPLER X SA-E WEIGHT OF THYROIDS

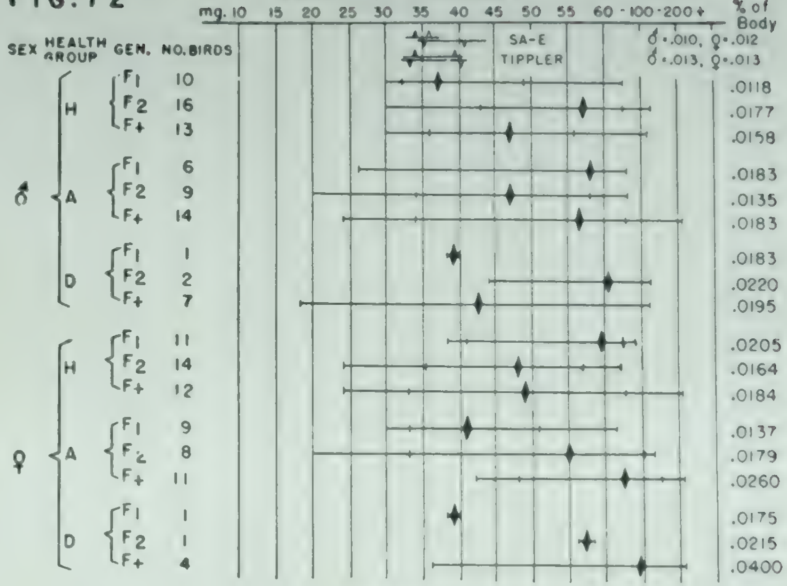


FIG. 73 HOMER X TIPPLER WEIGHT OF THYROIDS

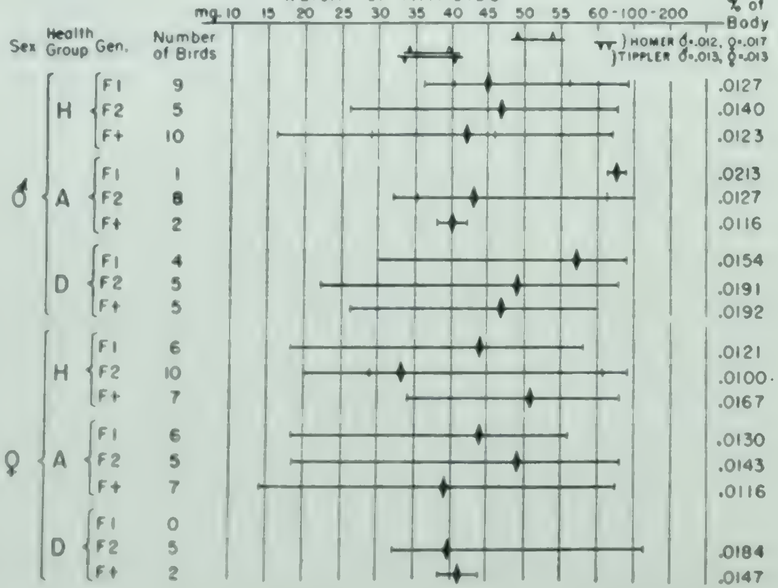


FIG. 74 TIPPLER X 267 WEIGHT OF THYROIDS

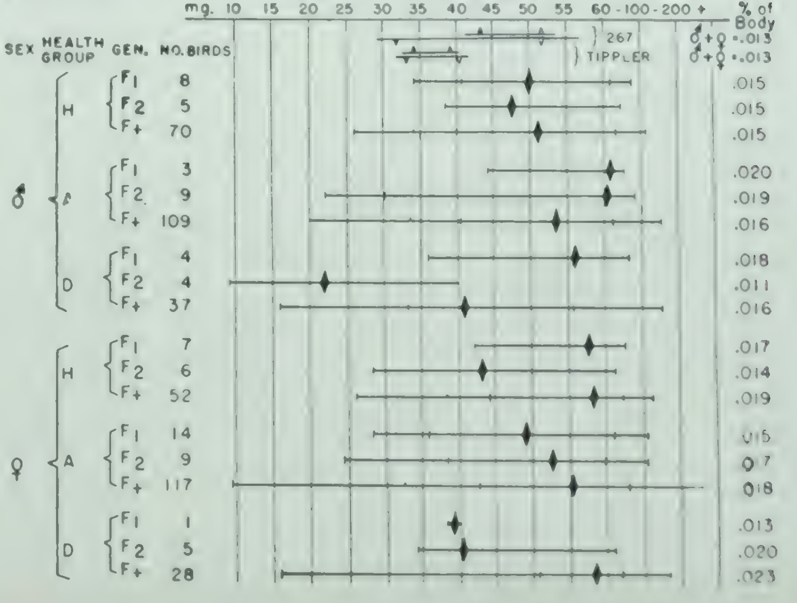


FIG 75

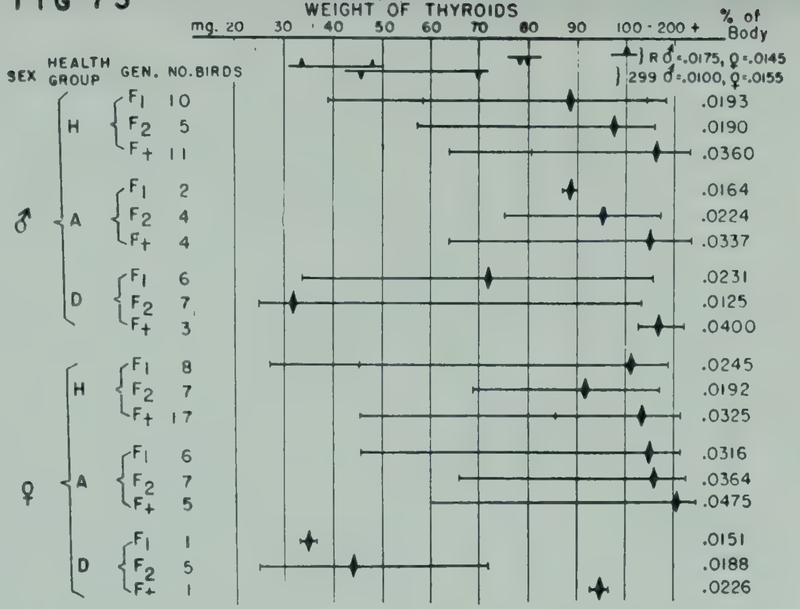


FIG.76

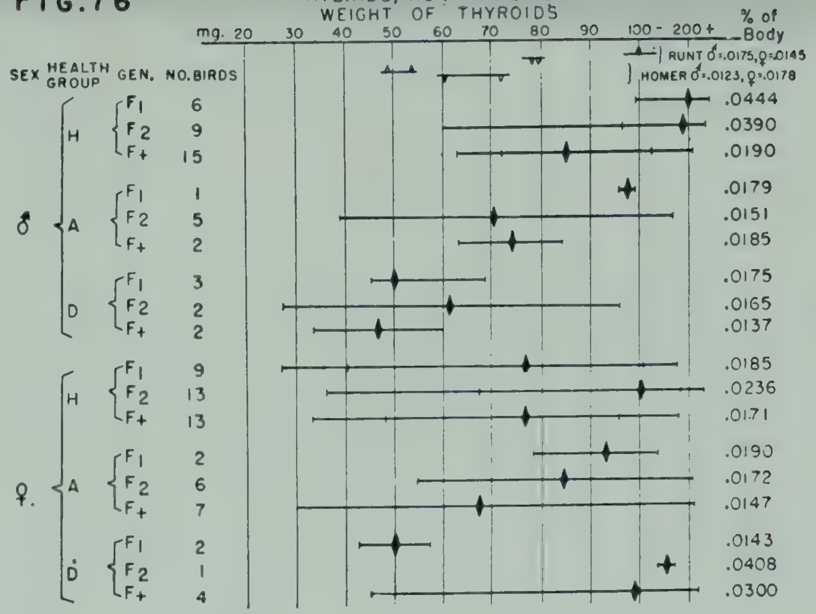


FIG.77

RUNT X SA-E

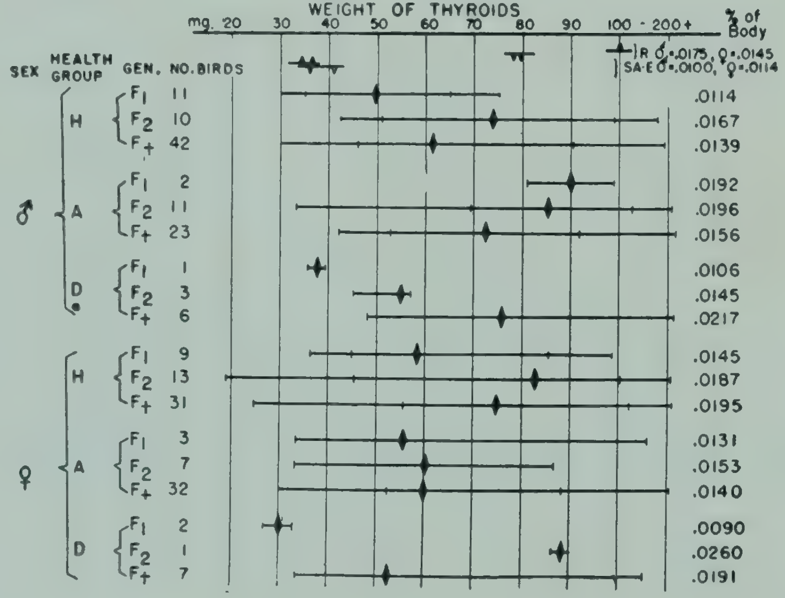


FIG.78

RUNT X MAGPIE

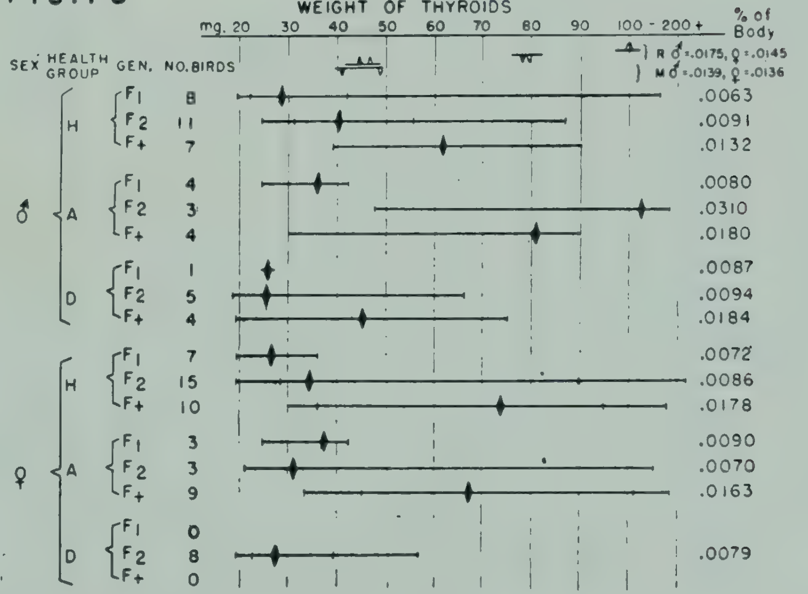
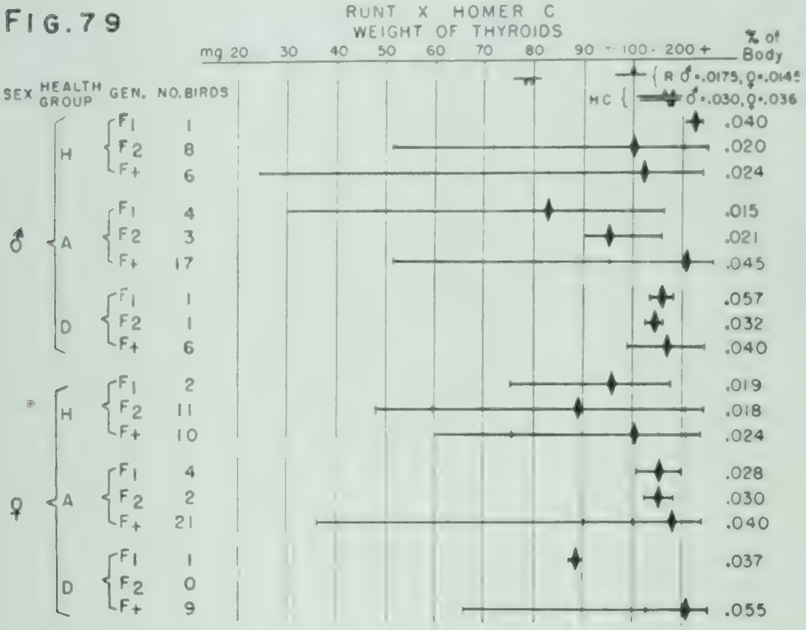


FIG. 79



The most important fact derivable from the tabulated data is that the thyroids of some dove races functioned at high and others at distinctly low levels. Heat production in race *75* exceeded that in race *62* by 17 per cent and that in race *67* by 14 per cent; the excess in race *N2* over that in race *OT* was 10 per cent; race *51* exceeded race *36* by 10 per cent, and race *W* exceeded race *62* by 12 per cent. These data show beyond question that genetic (racial) factors placed heat production in races *75*, *N2*, *51*, and *W* on a plane distinctly higher than that found in races *62*, *36*, *OT*, and *67*. In view of other known facts concerning these doves and various other species, it seems probable that differences in thyroid functioning are chiefly responsible for these differences in basal heat production. Certainly both thyroid type and B.M.R. were fixed genetically in several races.

With some notable exceptions, small thyroids are here shown to be thyroids with a high level of activity. Races *75*, *N2*, and *51* had small thyroids, and race *W* had thyroids which apparently were of intermediate or large size; these 4 races had higher levels of basal heat production than any other dove races. Again, races *62* and *72* had large thyroids, but they are found in the lower half of the list which ranks races according to rate of heat production. Similarly, among the pigeons Magpies and Tipplers (smallest thyroids) show highest, and Runts (large thyroids) show very low rates of heat production. It should be noted that the tabulation presented here gives heat production in terms of weight only, and that surface area is wholly disregarded; this method assigns much lower values to the largest breeds than does a calculation based on surface area. In the case of races *36* (doves) and *267* (pigeons), however, low thyroid weight was also associated with low metabolic rate.

Finally, inspection of the tabulated data reveals that the rate of heat production of hybrids is usually influenced by the rate found for both the parental races. In addition, particularly in crosses of the well marked breeds of pigeons, hybridity itself apparently sometimes tends to increase the metabolic rate.

TABLE 3

YEARLY AVERAGE BASAL HEAT PRODUCTION (CALORIES PER KILOGRAM PER HOUR) AT 30° C. OF RACES AND HYBRIDS OF DOVES AND PIGEONS (SEXES COMBINED)

RING DOVES				PIGEONS			
Race	Calories	Hybrid	Calories	Race	Calories	Hybrid	Calories
75	5.13	NE × N2	5.20	SA-R (scr.)	4.86	M × 299	4.30*
		44 × N2	5.19				
N2	5.07	72 × 75	4.98	Magpie	4.30*	T × SA-E.	4.27
		36 × B	4.98				
51	4.92	B × 72	4.89	Tippler	4.18	H × T	4.23
		Misc.	4.88				
W	4.91	N2 × 63	4.87	Homer	4.14	SA-E × 267	4.16*
		75 × B	4.85				
63	4.84	63 × 51	4.84	SA-E (nor.)	4.14	H × 267	4.14*
		36 × N2	4.81				
B	4.73	11 × 62	4.76	SA-R (atax.)	4.02	T × 267	4.03
		B × 62	4.73				
NA	4.68	36 × 72	4.70	SA-R (nor.)	4.01	R × H	3.98*
		72 × 63	4.70				
Misc.	4.65	65 × 163	4.65	White King	3.87	299 × R	3.94*
		62 × 75	4.64				
72	4.62	NA × 72	4.62	Runt	3.56	R × SA-E.	3.88
		63 × 44	4.62				
67	4.50	N2 × 62	4.61			C × HC	3.86*
		36 × 62	4.53				
OT	4.48	72 × OT	4.53			R × HC	3.82*
		72 × 62	4.52				
36	4.47†	63 × OT	4.46			R × M	3.78*
		67 × 72	4.46				
62	4.38	63 × 62	4.43				

*This value is for three seasons only.
†In race 36 only males were measured.

THE THYROID IN STUDIES ON CONSTITUTIONAL FACTORS IN MAN

In connection with the data described above, reference should be made to the fact that in studies on constitutional factors in man, particularly on factors relating to disease, the role of the thyroid has been much emphasized by most authors. Many studies on this subject have been published, but only a few books which give useful references to the literature will be cited here.

Early and important contributions were made by Draper[22] and Bauer.[23] The phenomena studied by E. Jaensch[24] and W. Jaensch[25] have been accorded consid-

[22] Draper, G., Human constitution: A consideration of its relationship to disease (Saunders, Philadelphia, 1924). Also, Draper and others (Hoeber, New York, 1944).

[23] Bauer, J., Constitución y enfermedad: Patologia constitucional aplicada (Aniceto Lopez, Buenos Aires, 1944). (Reference to own earlier books.)

[24] Jaensch, E., Die Eidetik und die typologische Forschungsmethode (Leipsic, 1933).

[25] Jaensch, W., Psychophysische Konstitutionstypen. *In* Handwörterbuch d. med. Psychologie (Leipsic, 1930).

erable attention in Germany though much less elsewhere. Current comprehensive studies by Sheldon[26] and associates are in process of publication. A review of a large amount of this literature was written by Tucker and Lessa.[27]

Conclusions and Summary

We here record the result of an attempt to select and segregate strains (races) characterized by thyroids of different levels of size and functional activity from a population of ring doves whose grades of mongrelization and thyroid activity were apparently comparable to those observed in the human population of an American city.

Twenty-four pairs of doves were selected from more than 200 pairs whose ancestry and reproductive records were largely known; a few pairs were closely related or their progeny soon died, but a significant amount of data for the inheritance of thyroid size was obtained on the progenies of about 18 of these pairs. Some further selection for large or for small thyroid size was practiced on the offspring of some of these pairs. Data for thyroid weight were also obtained from 4 additional inbred progenies of pure ring doves.

Twenty-seven kinds of hybrids were obtained by crossing the progenies of the above-mentioned pairs (races). Results obtained from both the line breeding and the crosses demonstrate that different genetic factors for thyroid size had been segregated in this material.

Despite continuous effort to avoid or minimize thyroid enlargement (goiter) from environmental sources, such enlargement occurred following 1930 in most racial and hybrid types; this environmental effect, however, did not erase or seriously obscure the evidence for hereditary diversity in, and control of, thyroid size in these dove races.

Hereditary control of thyroid size at levels which may be characterized as high, intermediate, and low is recognizable in the data obtained from doves. The progenies thus differentiated may properly be called strains or races. Races *62*, *B*, *72*, and probably *65* and *11*, were characterized by large thyroids; races *75*, *61*, *29*, *NA*, *44*, *51*, and perhaps also *36* and *N2*, had small thyroids; other races had thyroids best described as of intermediate size, though evidence of their genetic and functional difference from other thyroid types was obtained only for races *63* and *67*.

Both high and low levels of thyroid size and function were found in races derived from pure *Streptopelia risoria* as well as in races containing admixture of another species in their ancestry.

In certain crosses an influence of both parental races on the thyroid size of the hybrids was evident.

In the dove races and hybrids studied, thyroid weight tended to vary directly with liver weight, but this relation was not constant.

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[26] Sheldon, W. H., S. S. Stevens, and W. B. Tucker, The varieties of human physique: An introduction to constitutional psychology (Harper, New York, 1940).

[27] Tucker, W. B., and W. A. Lessa, Quart. Rev. Biol., 1940, vol. 15, p. 265.

A different type of study was conducted on thyroid size in 7 long-established breeds of pigeons, and in their hybrids, reared under essentially identical environmental conditions. Four additional (local) types developed in this colony, partly involving certain additional breeds, were included in this study.

After 1930 environmental goitrogenic conditions seriously interfered with the investigation of hereditary control of thyroid size in pigeon races and hybrids.

The data obtained on these pigeon races nevertheless indicate that Runts, Homers *C*, and Carneaux differed from Tipplers and Magpies in a genetic factor or factors which permitted the development of goiter. Local races *267*, *299*, and *SA-E* had characteristically small thyroids.

In pigeon races and hybrids ascariasis was usually associated with increased thyroid weight; this form of parasitization is elsewhere shown to be associated with increased liver weight in pigeons.

Data for basal heat production confirm and extend the evidence for functional and genetic difference in the thyroids of many races of both doves and pigeons.

With some definite exceptions, illustrated in races *36* and *267*, low thyroid weight was associated with a high level of thyroid function as indicated by higher basal metabolic rate. In general, but with exceptions, measurements made on hybrids tend to show metabolic levels which are intermediate to those of the parental races; a few pigeon and dove hybrids apparently tend to have a higher metabolic rate than has either of the respective parental races.

4

THE UNEQUAL RESPONSE OF RACES TO PROLACTIN

INTRODUCTORY STATEMENT

Several races and hybrid types of doves and pigeons were found to differ markedly in the extent of the response of their crop sacs to injections of the hormone prolactin. The results of a systematic study of this point are presented here. This more formal part of the study was preceded by much experience which had clearly indicated that certain races and types were more responsive than others to the prolactin contained in some hundreds of pituitary preparations assayed in our laboratory. It may be noted that there could have been no conscious or purposeful selection for degree of responsiveness to prolactin in the foundation of our ring-dove races, because prolactin was first isolated[1] and recognized ten years after the races were established. These differences must have existed in the parental stocks; selection, followed by inbreeding, permitted us to identify and propagate these as strain or "racial" differences.

For those unacquainted with these facts it may be stated that the pituitary hormone prolactin performs a number of regulatory functions in all higher animals.[2] In the normal life of pigeons of both sexes, prolactin produces, in addition to other results, growth in the crop sacs. This growth is later accompanied by the secretion of the so-called "crop milk" from the inner wall of the crop sacs. Young pigeons are nourished exclusively on crop milk, regurgitated by their parents, during the first week or two of life.

Parts of the present data, together with other related data, were published earlier.[3] In that study the practical importance of race in the bioassay of prolactin was stressed; in the present study a somewhat different body of data will be examined for its bearing on the question of constitution or race. Incidentally, the present results merit additional consideration because they direct attention to a little-known aspect of genetic difference.

Although the fact itself is widely recognized, not much has been published concerning the relative responsiveness in bioassays of different races or strains of experimental animals. Acton and Bose[4] found that under injection of insulin or adrenalin the change in blood sugar level differed significantly in three breeds or races of Himalayan rabbits; these races had been derived in the process of segregating three color types. Cole and Harned[5] found two strains of rats in which glucose tolerance differed markedly, with one of the strains giving a diabetic curve. Rotter and Mecz[6] reported that albino guinea pigs are more sensitive to thyroid preparations than are pigmented guinea pigs. Light and Cracas[7] noted that in order to obtain equal growth responses in two strains of rats, it was necessary to give one strain (in their own colony) twice as much vitamin B_1 as the other. Copeland[8] found that hooded rats from the Wisconsin strain had a choline requirement significantly different from that of rats selected from the Wistar strain, and tests on the progeny of each strain proved that this difference continued through two generations. The minimum daily choline requirement per rat of the Wistar strain was approximately 4 to 6 mg. (on diet 31PMC), whereas the requirement per rat of Wisconsin strain on the same diet was above 10 mg. Nalbandov and Casida[9] found, and their report was confirmed by Munro and others,[10] that the immature testes of certain breeds of fowl (White Rock) respond more actively than those of others (White Leghorns) to injections of gonadotrophin.

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[1] Riddle, O., R. W. Bates, and S. W. Dykshorn, Proc. Soc. Exper. Biol. and Med., 1932, vol. 39, p. 1211; Riddle, O., R. W. Bates, and S. W. Dykshorn, Amer. Jour. Physiol., 1933, vol. 105, p. 191.

[2] Riddle, O., Jour. Amer. Med. Assoc., 1940, vol. 115, p. 2276.

[3] Bates, R. W., O. Riddle, and E. L. Lahr, Amer. Jour. Physiol., 1939, vol. 125, p. 722.

[4] Acton, H. W., and J. P. Bose, Indian Jour. Med. Res., 1927–1928, vol. 15, p. 89.

[5] Cole, V. V., and B. K. Harned, Endocrinology, 1938, vol. 23, p. 318.

Perhaps racial difference in responsiveness of tissues—if responsiveness of tissue proves to be the essential factor in the above-mentioned cases—is involved in many genetic differences. The unequal milk-producing abilities of well known breeds of cattle and the dissimilar egg-laying abilities of various races of fowl are recognized racial variables; these differences probably reflect either an inherently different endocrine status or a differing responsiveness of tissues, often along with other aspects of genetic difference. Riddle, Bates, and Lahr[11] found that injections of prolactin into laying fowl produced broodiness, and noted that hens from genetically nonbroody races showed a marked quantitative difference in response (clucking only) from hens of "broody" races. The fact that a genetic basis exists for this difference in response of fowl to prolactin may have a bearing upon an interpretation of the differences in response here observed in the crop sacs of pigeons.

The few pigeon races utilized in these tests ranged in body weight from 280 to 600 gm.; the dove races differed little in body weight. Because of the narrow age range (6 to 10 weeks after hatching) of birds suitable for these tests, and because only small numbers of birds of each race were available at any given time in our colony, the present tests were limited to a small number of birds in each racial group. The difference found (duplicate tests, usually) between several types which gave a high response and several which gave a low response is, however, of such magnitude as to render the results significant despite the small numbers of birds used.

A single prolactin preparation (no. 296) containing 4 units per milligram was used in all tests. The injection procedures were identical with those much used in this laboratory for assaying the prolactin content of pituitary preparations; crop-sac weights can therefore be converted directly into equivalent unitage of prolactin by means of an assay table published elsewhere.[12] Since the practical importance of the racial difference lies in its effect on assay values, and since relative responsiveness of crop sacs is best measured on a basis of units, the results obtained for the various races have been so tabulated as to give comparisons in terms of units as well as in terms of actual crop-sac weights. The unit of prolactin was fixed arbitrarily, but the (Riddle-Bates) unit used in these tests is only slightly larger than the present international unit. Until the present tests were concluded it was not realized that the highest dosage used (25 times the lowest dose) was too high for satisfactory use with some races. For this reason the values obtained at the lower level of dosage usually provide the more reliable comparisons.

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[6] Rotter, G., and M. Mecz, Arch. f. exper. Pathol. und Pharmakol., 1932, vol. 166, p. 649.

[7] Light, R. F., and L. J. Cracas, Science, 1938, vol. 87, p. 90.

[8] Copeland, D. H., Proc. Soc. Exper. Biol. and Med., 1944, vol. 57, p. 33.

[9] Nalbandov, A. V., and L. E. Casida, Endocrinology, 1940, vol. 27, p. 559.

[10] Munro, S. S., I. L. Kosin, and E. L. Macartney, Amer. Naturalist, 1943, vol. 77, p. 256.

[11] Riddle, O., R. W. Bates, and E. L. Lahr, Amer. Jour. Physiol., 1935, vol. 111, p. 352.

Experimental Results

The results obtained from several ring-dove races or hybrid types following injections of prolactin at *two* dosage levels are shown in tables 4 and 5. The races are arranged in the order of their responsiveness as this was indicated by the crop-sac weights obtained. With the notable exception of race *W*, this sequence (for those races which were treated at both levels) is essentially the same at both levels of dosage. There is almost no overlap of the data obtained from individuals belonging to races at the extreme top and those at the extreme bottom of the two tables. The maximum racial difference in response, in terms of units, is a 24-fold difference under high dosage (table 4) and an 8-fold difference under low dosage (table 5). The 8-fold difference is to be regarded as the actual difference in view of the consideration mentioned in the preceding and following paragraphs.

Smaller numbers of birds of 11 of the races (or hybrids) listed in tables 4 and 5 were further tested at *four* additional dose levels (0.1, 1.6, 4.0, and 16.0 mg. daily) of the same prolactin preparation (no. 296). It does not seem necessary to publish the results of these more diversified and space-consuming tests; those results substantially confirm the data of tables 4 and 5.

Most of the data in table 4 were obtained in 1934, and those in table 5 were obtained a year later. On the basis of the data of table 4 the *N2* × *62* hybrids and race *W* were selected (early in 1935) as representative of high-responding and low-responding races, respectively, and their response under variable and graduated prolactin dosage was made the subject of a special test. It turned out that race *W* gave an extremely low response only when tested at high levels of dosage. The results are shown in figure 79*a*. The control, or unstimulated, weight (usually 300 to 400 mg.) of the crop sacs of doves is indicated on this graph. It was found that when crop-sac weights are plotted against the logarithm of the prolactin dosage, the experimental points fall along a straight line of characteristic slope—this slope being independent of age and, after correction for differences in

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[12] Riddle, O., and R. W. Bates, chap. 20, p. 1088, *in* Allen, E. (ed.), Sex and internal secretions (2d ed., Williams & Wilkins Co., Baltimore, 1939).

TABLE 4

Differences in response to high dosage of prolactin in races of ring doves. Ten milligrams (40 units) of no. 296 injected intramuscularly daily for 4 days.

Race	No. of birds	Crop-sac weight (mg.)				Response obtained	
		Minimum	Maximum	Average	σ_{mean}	In units	Ratio to 160 units
63 × 44	5	2,010	2,505	2,320	± 91	360	2.2
N2 × 62	9	1,630	2,475	2,060	± 75	165	1.0
B × 62	4	1,665	2,185	1,940	±115	113	0.75
N2	4	1,535	2,380	1,890	±177	98	0.65
72	7	1,650	2,470	1,880	±108	94	0.59
63	14	1,270	2,185	1,810	±108	75	0.47
62	6	1,410	2,055	1,800	± 87	74	0.46
75	4	1,470	2,035	1,690	±123	53	0.35
NA × 72	7	1,195	2,215	1,590	±130	39	0.24
63 × 72	7	1,290	1,895	1,580	± 82	37	0.23
B	4	1,295	1,850	1,560	±105	35	0.23
62 × 75	8	1,060	2,315	1,560	±144	35	0.23
51 × 63	6	1,230	1,755	1,540	± 87	33	0.21
NA	3	1,075	1,685	1,480	±186	28	0.18
51	5	1,290	1,935	1,440	±123	24	0.15
W	8	925	1,655	1,270	± 72	15	0.09

TABLE 5

Differences in response to low dosage of prolactin in races of ring doves. Four-tenths milligram (1.6 units) of no. 296 injected intramuscularly daily for 4 days.

Race	No. of birds	Crop-sac weight (mg.)				Response obtained	
		Minimum	Maximum	Average	σ_{mean}	In units	Ratio to 6.4 units
63 × 44	5	1,095	2,025	1,440	±161	24	3.8
N2 × 62	5	955	1,495	1,310	±105	14	2.2
63 × OT	5	865	1,445	1,195	±102	11.5	1.8
N2	4	915	1,375	1,102	±179	8.6	1.4
B × 62	7	645	1,945	1,090	±183	8.4	1.3
62 × 63	5	945	1,165	1,085	± 49	8.3	1.3
63 × 72	5	765	1,385	1,000	±104	6.3	0.98
W	7	705	1,180	970	± 70	5.7	0.89
72	6	650	1,160	945	± 73	5.3	0.83
63	5	670	1,425	945	±128	5.3	0.83
NA × 72	5	730	1,030	865	± 56	4.2	0.66
51 × 63	5	520	1,070	845	±100	3.9	0.61
72 × 75 × B	5	605	1,150	840	±103	3.8	0.59
65	5	665	905	800	± 43	3.4	0.53
72 × OT × NA	5	500	1,020	740	± 98	2.9	0.45

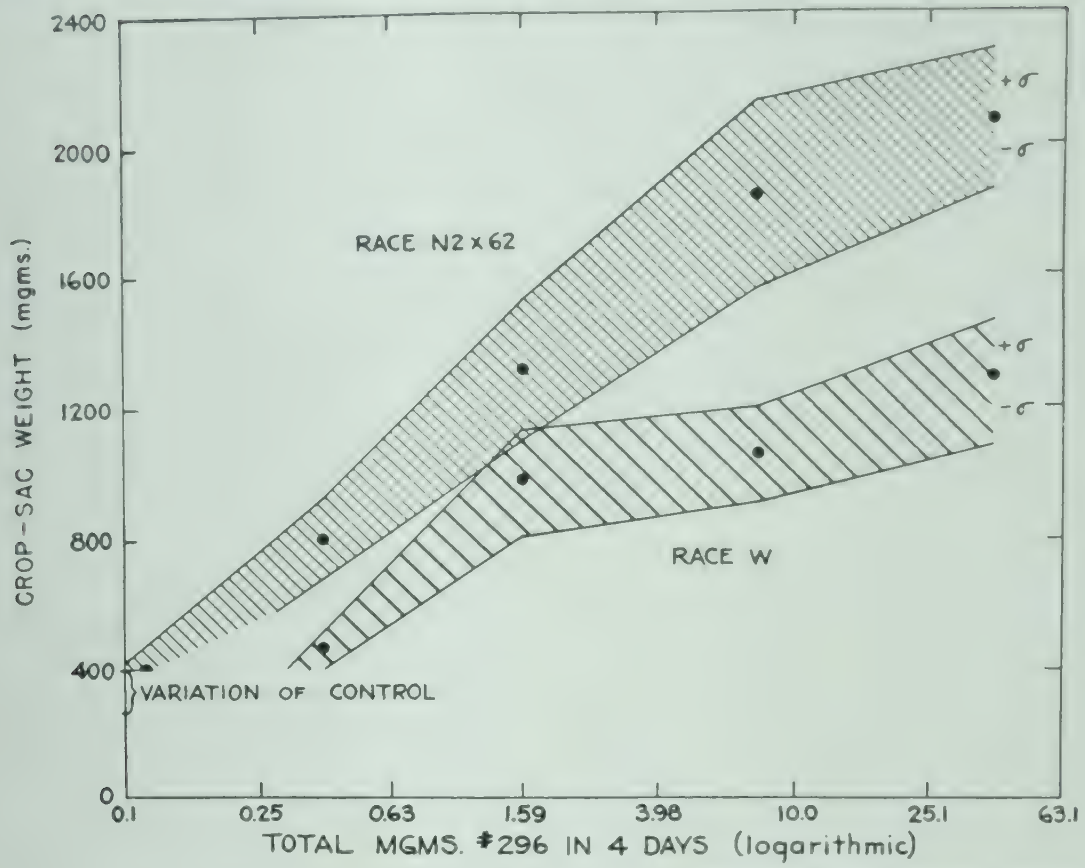

Fig. 79*a*. Response of 2 races (types) of ring doves to prolactin. Points represent average weights of crop sacs from 4 to 9 doves.

body weight, also quite the same for pigeons as for ring doves. All the points for race *N2 × 62*, with the exception of the one for the highest dosage, fall along a line with the characteristic slope. In the case of race *W* only the points for the two lowest dosages (totals of 0.4 and 1.6 mg.) fall along a line with the usual slope; a further increase of the dosage by 5 times (to 8 mg.) did not appreciably increase the crop-sac weight, and an increase of the dosage by 25 times (to 40 mg.) increased the crop-sac weight little more than would be expected from an increase of dosage to 4 mg. At the two low levels of dosage, race *W* required 2.5 times more prolactin than did race *N2 × 62* to produce equal crop-sac weights. One aspect of the racial difference between these two types may be expressed in the following way: Race *W* obviously is of no value for quantitative assay of prolactin except at low dosage levels of only 4 to 5 times the minimal stimulating dose for race *W*. Race *N2 × 62* can be used for assaying at dosage levels up to 50 to 100 times the minimal stimulating dose for *N2 × 62*, a value which is 20 to 40 times the minimal stimulating dose for race *W*.

Four races of pigeons were tested at high and low levels of prolactin dosage, the higher dosage being 25 times the lower as in the case of doves. This dosage, however, was relatively less than for the doves, because of the greater body weight of the pigeons. Table 6 presents the data obtained from pigeons. Because of the

TABLE 6

DIFFERENCES IN RESPONSE TO TWO DOSAGE LEVELS OF PROLACTIN IN SIX RACES OF PIGEONS. LOW DOSAGE (0.5 MG. OR 2 UNITS) AND HIGH DOSAGE (12.5 MG. OR 50 UNITS) OF NO. 296 INJECTED INTRAMUSCULARLY DAILY FOR 4 DAYS. ACTUAL DOSAGE WAS PROPORTIONAL TO BODY WEIGHT.

Race	No. of birds	Body wt. (gm.)	Total units per 450 gm.	Crop-sac wt./450 gm. (mg.)				Response obtained	
				Minimum	Maximum	Average	σ_{mean}	In units	Ratio to 200 or to 8 units
White King	9	598	200	4,200	7,050	5,800	±378	330	1.7
	5	556	8	3,180	4,500	3,890	±231	47.2	5.9
Homer (own)	6	358	200	4,500	8,410	5,970	±543	395	2.0
	5	357	8	1,980	3,870	2,910	±361	17.3	2.2
Carneau*	5	439	8	1,500	3,360	2,520	±390	11.5	1.4
Homer*	5	394	8	1,625	2,280	2,070	±120	7.3	0.91
T × 267	12	309	200	3,150	5,130	4,470	±238	85	0.43
	5	318	8	1,125	1,905	1,545	±141	4.3	0.54
Tippler	9	292	200	3,660	5,550	4,490	±183	87	0.44
	5	263	8	1,155	1,640	1,410	±111	3.7	0.46

*Birds purchased from Palmetto Pigeon Plant, Sumter, S. C.

variation in body weight among pigeon races, the crop-sac weights have been calculated to equivalent body weights (450 gm.). The birds were injected with amounts of prolactin in proportion to their body weight. Under low dosage, a maximal racial difference (in units) of more than 12-fold was found among the 6 types tested. Three of the 4 races which were tested at both levels of dosage show differences in response remarkably near the expected difference. White Kings, however, were found (like race *W* among doves) to be in the region of their maximal response on the low dosage level; it is only because they were the most responsive race of pigeons tested that they still show, at the high level of dosage, their high relative position in the table.

The observed racial differences relate both to the amount of hormone which gives essentially a maximal response, and to the degree of response obtainable at low levels of dosage. For the quantitative assay of prolactin by the crop-sac method it was necessary therefore to determine for any race the useful range over which crop-sac weight increases in proportion to dosage, and also to establish the approximate racial correction factor. These two aims were accomplished simultaneously by standardizing the race against a standard prolactin preparation. The ratios given in the last column of tables 4 to 6 are such racial correction factors. It may be seen (table 6) that 5 Carneau pigeons, tested with preparation no. 296, indicated that this factor was 1.4. Larger numbers (30) of Carneaux, injected with other prolactin preparations, indicated that their racial factor is 1.2.

It is because the Riddle-Bates unit of prolactin was based on crop-sac data obtained from groups of doves belonging to several races (selected at random) that the data from the dove races of tables 4 and 5 fall both above and below the theoretical value of that unit.

The ring dove types whose crop-sac weights responded most strongly to injected prolactin were *63* × *44*, *N2* × *62*, *63* × *OT*, *N2*, and *B* × *62;* weakest responses were obtained in races *65*, *51* × *63*, *NA* × *72*, *NA*, and *51*. Two pigeon types, White Kings and our own strain of Homers, gave an extremely high response; Tipplers and *T* × *267* gave an extremely low response. Although White Carneaux were intermediate to the four above-named types, still other tests (in routine assays) showed repeatedly that values obtained for *groups* of Carneaux distinguished them from any of the other types recorded on table 6.

The various breeds of pigeons used show marked differences of body weight. The data of table 6 give strong evidence for an association of the body size of races with high sensitivity of the crop sacs to prolactin. The values (from last column of table) obtained under low dosage show that, except in one group of Homers (our own), sensitivity to prolactin is directly associated with racial body weight; the largest breed is also the breed whose crop sacs are most sensitive to prolactin.

Discussion

Little or no evidence was obtained for a correlation of either heat production or thyroid weight with the crop-sac response. Among ring doves, however, greater gut length shows at least a partial positive correlation with greater responsiveness of the crop sacs. This correlation is perhaps sufficiently indicated in doves by the fact that the 5 most responsive types (*63* × *44*, *N2* × *62*, *63* × *OT*, *N2*, *B* × *62*) had mean intestinal indices (intestine/body weight) of 0.358, 0.394, 0.350, 0.403, and 0.366. These indices in the 5 types (*65*, *51* × *63*, *NA* × *72*, *NA*, *51*) giving apparently lowest crop-sac response were 0.337, 0.347, 0.338, 0.338, and 0.348. The body weights of the 6 pigeon races differ so much that the index used for doves is probably not applicable to them.

Adequate consideration of these data involves a point of high biologic interest. How is this difference in the response of the crop sacs to prolactin to be explained? Three possibilities are evident. First, the difference may rest solely upon an inherent difference in the responding (crop-sac) tissue in the various races; in this case an important and little-known type of genetic difference is involved. Second, the hereditary difference may relate solely to the factors or mechanisms that determine the concentration and persistence of the injected hormone in the blood stream; such mechanisms, particularly those controlling the rates of absorption and elimination, may be considered general mechanisms. A third possibility is that the observed difference rests both upon the responding tissue and upon such metabolic mechanisms.

Differences which may have something in common with those discussed above have been observed in individual human beings. Certain variations in the growth response (which also is a response largely under the control of the pituitary gland) seem to show different thresholds of response in the different tissues of the body. For example, it is well known that in most cases of acromegaly in man not all the tissues capable of responding actually do so. In relatively few cases do the viscera increase in size, and the jaws show overgrowth most readily. Of special interest in relation to the present question are the cases cited by Lichtwitz[13] in which the right jaw, but not the left, showed overgrowth. Here apparently is a true difference in tissue responsiveness, and this type of (bilateral) difference may well have a genetic basis, as have other better-analyzed characteristics involving inequality of the two sides of the body.

The adaptive or other significance of the very unequal responsiveness of dove and pigeon races to a hormone which is almost certainly essential to survival is now largely unexplored. Perhaps the association of degree of responsiveness with gut length, and with body weight in pigeon races, may serve as a guide to further inquiry. It must not be forgotten that these inequalities were segregated and propagated in our ring doves as racial characteristics; the existence of inequalities of this type and degree in animal populations is an impressive fact for studies on constitutional factors.

SUMMARY

Several dove and pigeon races were characterized by unusually high or low responsiveness of their crop sacs to the only hormone (prolactin) which has been found capable of stimulating growth and functioning in that tissue. The races and hybrid types identified with either of the two extremes of responsiveness are listed. Some races and hybrid types were not subjected to this test.

The observed racial differences relate both to the amount of hormone which gives a maximal response, and to the degree of response obtainable at low levels of dosage. For the latter, 8-fold (doves) and 12-fold (pigeons) differences were found.

There was no correlation of high or low responsiveness with metabolic rate or with thyroid size. On the other hand, extreme gut length shows at least a partial positive correlation with greater responsiveness of the crop sacs to prolactin. Moreover, with exception of one race (our Homers) of the six races of pigeons measured at low dosage, responsiveness was positively correlated with body weight.

It seems clear that these inequalities were segregated, in part, from individuals which were related and indistinguishable by usual methods of observation. Though the biologic significance of these widely different degrees of responsiveness is still largely unexplored, it is clear that they exist, that they are under genetic control, and that they were here established as racial characteristics.

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[13] Lichtwitz, L., Amer. Jour. Orthod. and Oral Surg., 1938, vol. 24, p. 3.

5

THE ESTABLISHMENT OF DOVE RACES WITH UNEQUAL INTESTINAL LENGTH; WITH A CONSIDERATION OF UNEQUAL PITUITARY SIZE IN DOVE AND PIGEON RACES

The present study had the immediate purpose of obtaining an answer to the following question: Within a population of ring doves whose grade of mongrelization seems quite comparable with that observed in the human population of an American city, is it possible to establish races with unequal intestinal length? It was hoped, and considered probable, that a positive answer would provide material from which it would be possible to obtain much-needed information concerning functions and relations of the anterior pituitary gland. It should be stated at once that this hope rested largely upon a single item of information obtained in 1921 from a personal conversation with Dr. Lewellys F. Barker. The author was told that Dr. Barker's observations in the dissecting room had made it fairly evident that extra length of intestine in man is associated with large or extra large size of hypophysis. Since our original wish was to select and establish "pituitary" races, and our preliminary tests on weighing the relatively inaccessible pituitaries of doves had indicated the difficulties and labor involved in a direct approach to this problem, Dr. Barker's observation led us to select for extremes of intestinal length. In part this selection was done to obtain races with extremes of intestinal length, but in part it was done to increase the chances of obtaining races with extremes of pituitary size. The direct study of pituitary size in the various races has been less extensive than was planned, and less extensive than is desirable.

HISTORICAL

Further encouragement in the undertaking of this study was obtained from the fact that Hatai[1] and Jackson[2] had found that female pituitaries are heavier than male pituitaries in albino rats, and that a partial study[3] of the matter in common pigeons had led to a like result. Two preliminary reports have considered parts of the present data for intestinal length in their relation to other data obtained for pituitary weights. In the first of these reports Riddle and Flemion[4] noted that in each of ten groups of ring doves (total of 1157 doves) the intestines of females were longer (3.2 to 14.6 per cent) than those of the corresponding males despite slightly greater body weight in the males. Also included in this publication were a few pituitary weights for pigeons which indicated (confirming McCarrison) that, in relation to body weight, the female pituitary is slightly heavier than that of the male. The second report, by Riddle and Nussmann,[5] showed that the pituitaries of both pigeons and doves are absolutely and relatively heavier in the females than in the males of the same race. Moreover, in several races of both pigeons and doves it was found that the females have the longer intestinal tracts. For these two groups of birds it thus was shown that the *sex* with the longer intestine has the larger pituitary; but it was also noted that between *races* this type of association does not prevail. These data (tables 9, 10) are reproduced and discussed later in this chapter.

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[1] Hatai, S., Amer. Jour. Anat., 1913, vol. 15, p. 87.

[2] Jackson, C. M., Amer. Jour. Anat., 1917, vol. 21, p. 321.

[3] McCarrison, R., Indian Jour. Med. Res., 1919, vol. 6, p. 550.

[4] Riddle, O., and F. Flemion, Endocrinology, 1928, vol. 12, p. 203.

Other observers have shown that the female hypophysis as a whole, and particularly its anterior lobe, is larger than that of the male in rabbits, rats, cattle, and man; in hibernating woodchucks (*Marmota monax*) it seems that the reverse is true.[6] Various clinical observations have indicated that hypersecretion of the anterior lobe of the pituitary is associated with splanchnomegaly, but those studies will not be cited here.

Maucci[7] measured the intestines and weighed the pituitaries of 12 male and 12 female cadavers. From the results it was concluded that a heavier hypophysis is associated with a longer intestine, but in this material the females apparently had neither larger pituitaries nor longer intestines than the males. Moreover, Maucci was unable to associate either unusual length of intestine or unusual pituitary weight with one or another constitutional type. There is reason to believe that Miloslavich has published data of the type just reviewed, but it has been possible to find only the first of his publications dealing with intestinal length. That study[8] deals with length of the large intestine in ethnic groups in middle and southeastern Europe. This organ was abnormally long (hyperdolichocolon) in 60 per cent of Russians, in 25 per cent of Ruthenians, and in only 5.5 per cent of Germans. Mode of life (environment) was believed to account for much, though apparently not all, of the differences observed.

Endocrines Related to Intestinal Length in Pigeons

Although intestinal length in doves and pigeons may not be correlated with large or small pituitary size, as indicated in a study[5] reviewed above, this lack of correlation cannot be considered evidence that no pituitary product specifically affects intestinal length. We now know, as we did not know in 1922, that the anterior pituitary produces not one, but a still undetermined number of hormones. It will now be noted that prolactin has given clear evidence of specific ability to stimulate growth in the intestinal tract of doves and pigeons. On the basis of this evidence, intestinal length can be regarded as a constitutional feature which is partly endocrine-controlled; and it is possible that the genetic control of intestinal length, made evident by the present data, is exercised either upon the output of prolactin by pituitary cells or through a modified responsiveness of intestinal tissues to prolactin.

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[5] Riddle, O., and T. C. Nussmann, Anat. Rec., 1933, vol. 57, p. 197.

[6] Rasmussen, A. T., Endocrinology, 1928, vol. 12, p. 129; Anat. Rec., 1933, vol. 55, p. 139.

[7] Maucci, O. C., thesis, Instituto della Anatomia, R. Università di Genova, 1932.

[8] Miloslavich, E. L., Amer. Jour. Phys. Anthropol., 1925, vol. 8, p. 11.

First of all, it is not negligible that two restricted areas (crop sacs) of the alimentary canal are stimulated to growth and special functioning only by prolactin;[9] and in these birds the production of crop milk, thus controlled by the pituitary, is essential to the rearing of young. Both normal and hypophysectomized young Carneau pigeons have contributed significant evidence that the lower intestinal tract (from gizzard to anus) also gives a specific response to prolactin. At 3 weeks after hatching, young Carneau pigeons show higher weights of crop sacs (1670 ± 70 mg. standard error) and longer intestines (117.8 ± 2.2 cm.) in relation to body weight (ratio = 0.393) than at any later phase of growth.[10] Though heavy food consumption at and preceding this period is probably partly responsible, the whole of the evidence indicates that at this period the birds' own pituitaries produce unusual quantities of prolactin and that this hormone is partly responsible for these overgrowths.[10] When these birds were somewhat older, and in growth stasis, the administration of prolactin was followed by a resumption of body growth and by overgrowth in the intestines (and liver).[10] In some groups of birds hypophysectomized at the age of 2 months, and injected for 10 days thereafter with prolactin, intestinal length (and empty weight) was increased (by 10 to 27 cm. or more than 10 per cent) without an increase in food consumption.[11]

Environmental Agents Affecting Intestinal Length

Some of the environmental conditions that may possibly affect intestinal length in pigeons have not been studied intensively in these animals. What is known, however, about these and other animals indicates that the more important factors are nature and amount of food, and ascariasis and other disease. Season was found[12] to have but a slight influence in ring doves and it is disregarded entirely in the present summaries. The slight apparent increase observed during autumn and winter can probably be accounted for by an increase in food consumption at these periods of lower external temperature. In groups of young Carneau pigeons, studied at slightly less than 2 months, moderate "stuffing" (overfeeding) during 10 days was observed to lengthen the intestine to the extent of about 3 cm., whereas complete witholding of food for a like period produced a decrease of about 10 cm. (10 per cent).[11] As earlier noted, all birds were fed a mixture of dry grain which was not the same for doves as for pigeons. The components of this mixture did not vary greatly during the test, and when a variation occurred it was shared by all members of the colony.

[9] Riddle, O., R. W. Bates, and S. W. Dykshorn, Amer. Jour. Physiol., 1933, vol. 105, p. 191.

[10] Bates, R. W., O. Riddle, E. L. Lahr, and J. P. Schooley, Amer. Jour. Physiol., 1937, vol. 119, p. 603.

[11] Schooley, J. P., O. Riddle, and R. W. Bates, Amer. Jour. Anat., 1941, vol. 69, p. 123.

[12] Riddle, O., Endocrinology, 1929, vol. 13, p. 311.

Diseased and dead birds obviously include a high percentage of all those individuals which had been subjected to a maximum of environmental stresses. Data obtained from these birds are given mainly to accomplish the presentation of all our measurements. It was noted above that ascariasis was earlier found to be associated with a measurable lengthening of the intestines of ring doves. Birds thus affected are here given separate classification, except in the case of pigeon hybrids, where it was found that ascariasis produced no consistent effect. The data summarized here provide extensive information concerning the effect of ascariasis on intestinal length in both doves and pigeons.

Data for Dove Races and Hybrids

A graph (fig. 80) provides a general view of the results obtained for both sexes of 17 races. Only healthy birds and those with ascariasis are included. The great majority of doves have intestines 50 to 60 cm. in length, with a ratio of intestinal length (in cm.) to body weight (in gm.) varying around 0.35. This graph indicates that races *N2*, *44*, *6*, *75*, and *36* had relatively long intestines, and races *OT*, *78*, *72*, and *B* had relatively short intestines.

Percentile analyses of all data obtained for 18 races are given in figures 81 to 86. Here data for the sexes and for the three "health" groups are given separately. The results clearly demonstrate that in females the intestines are relatively, and usually also absolutely, longer than in males. The ratio of the intestinal length to the body weight is recorded for all groups. Perhaps more than coincidence is involved in the fact that the 2 races (*N2* and *44*) which had longest intestines did not show the usual sex difference in body weight. Both these races did show the usual sex difference in length of intestine.

Percentile analyses of data for the 10 hybrid types for which greatest numbers are available are given in figures 87 to 96. In these cases, data for F_1, F_2, and F_+ are separately analyzed, and healthy birds and those with ascariasis are included. Data obtained from 32 additional (minor) crosses are shown, but the various generations are not treated separately (figs. 97–100).

The data cited show that both in dove races and in hybrids ascariasis was often but by no means always associated with greater median length of intestine. The increase, when present, was rarely as much as 3 cm. The actual median values obtained from dead and diseased birds are quite similar to the values from healthy birds, although the ratios to body weight were usually increased considerably because of the frequent emaciation of dead and diseased birds.

Distributions of intestinal-length frequencies tend to be normal or to show slight positive skewness. Coefficients of dispersion for healthy and ascariasis groups are in most cases very similar. Race 75 is a notable exception, since the coefficient of dispersion for birds with ascariasis is there about twice that for healthy birds. The reverse tendency is observed in race *N2*, but the data are probably less significant. For dead and diseased birds the coefficient is usually similar to that for healthy birds. Racial variations in coefficients of dispersion do not appear to be markedly correlated with medians for either intestinal length

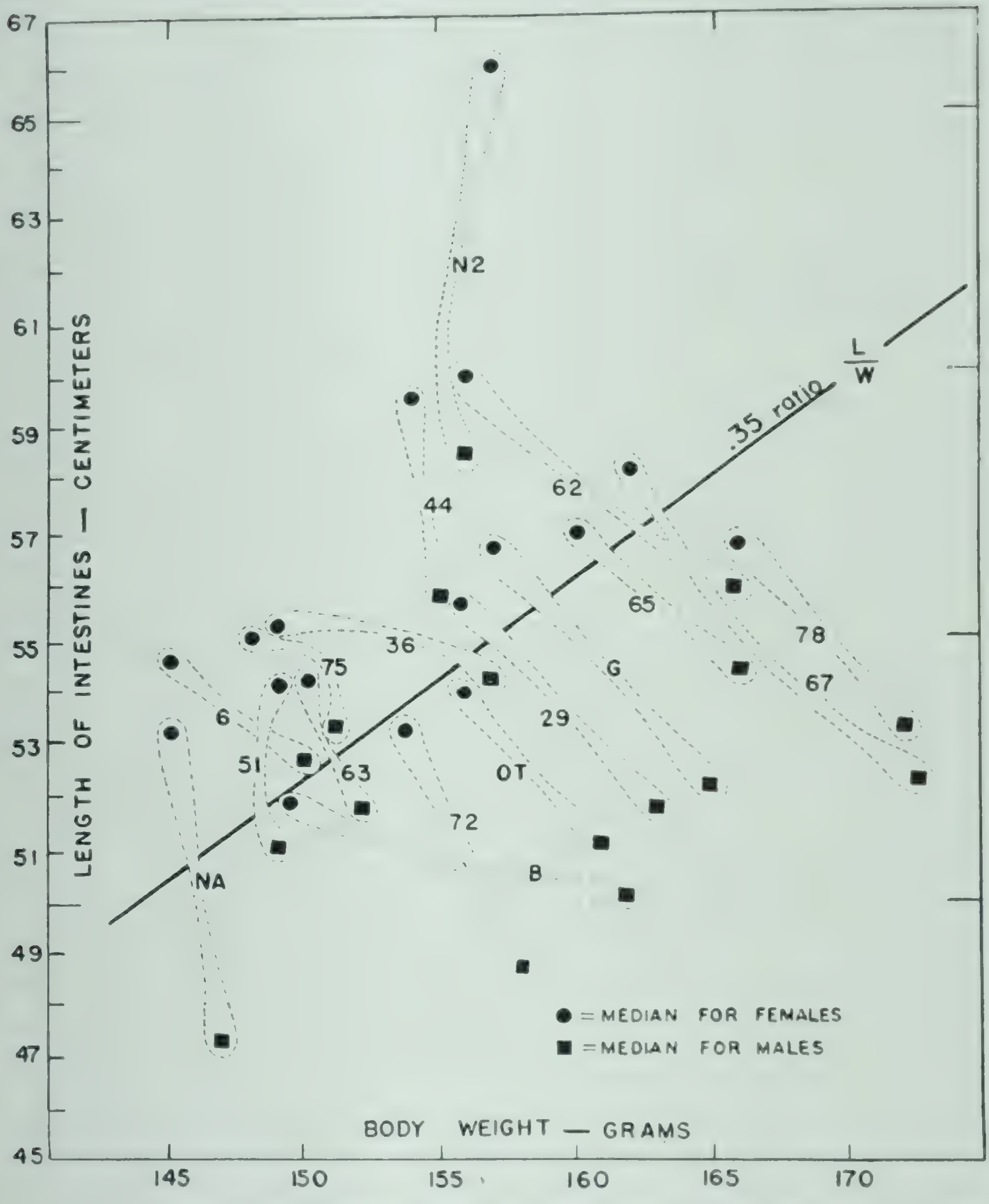


Fig. 80. A survey of both intestinal length and body weight in the two sexes of 17 races of doves. The data were obtained from healthy adults, including those with intestinal parasites (ascariasis).

or body weight. The lowest coefficient of dispersion (about 0.05) is found in *NA* males; the highest (about 0.10) in race *6* females. Sex differences in the value of this coefficient seem negligible.

The actual differences between racial medians for intestinal length are rather small in most or typical cases. There is a slight tendency for the intestines to be relatively shorter in the heavier races. The extreme types are represented by races

FIG. 81

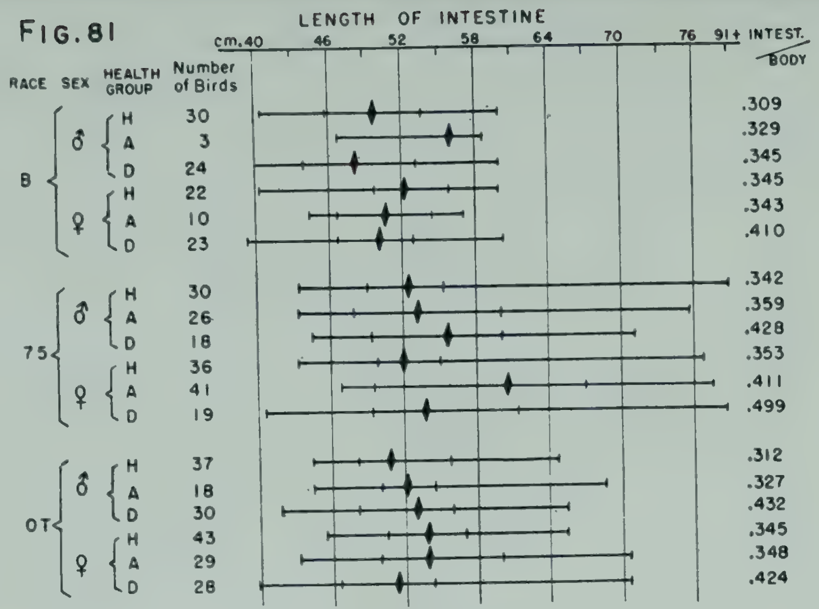


FIG. 82

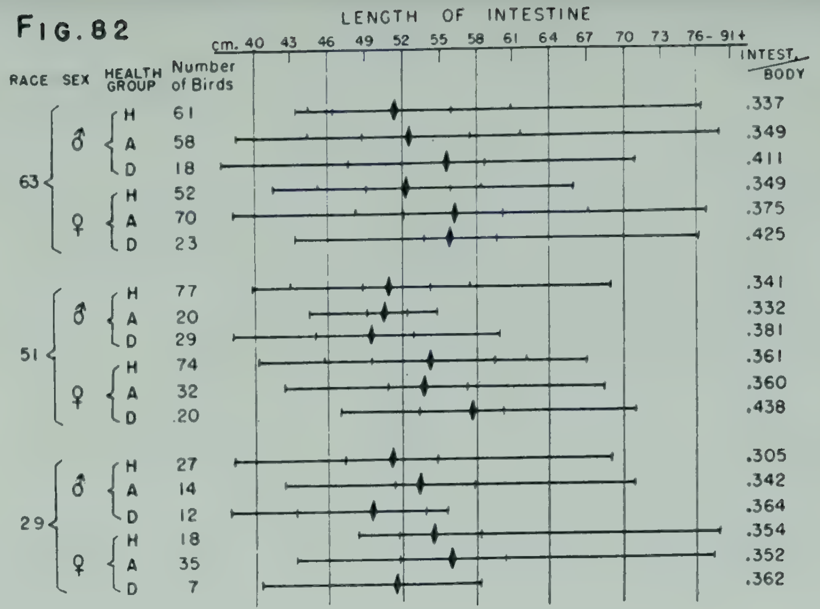


FIG. 83

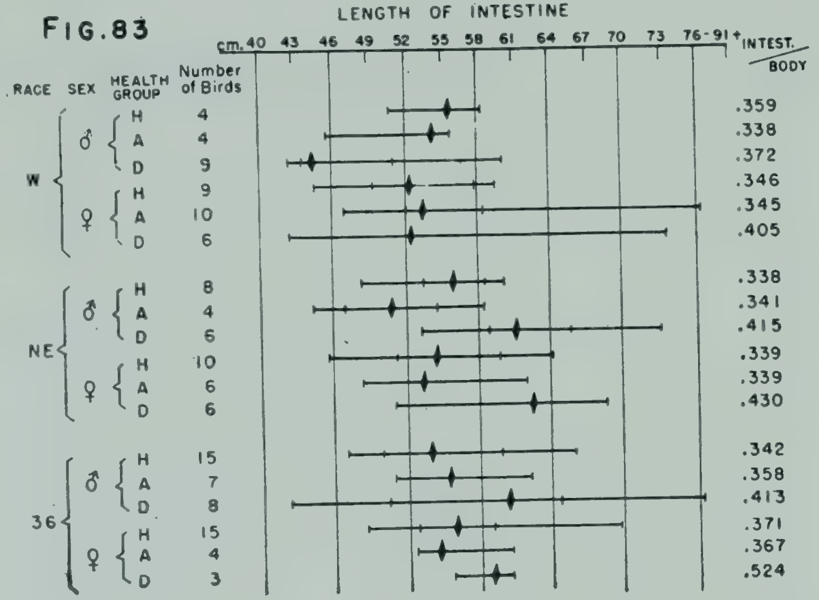


FIG. 84

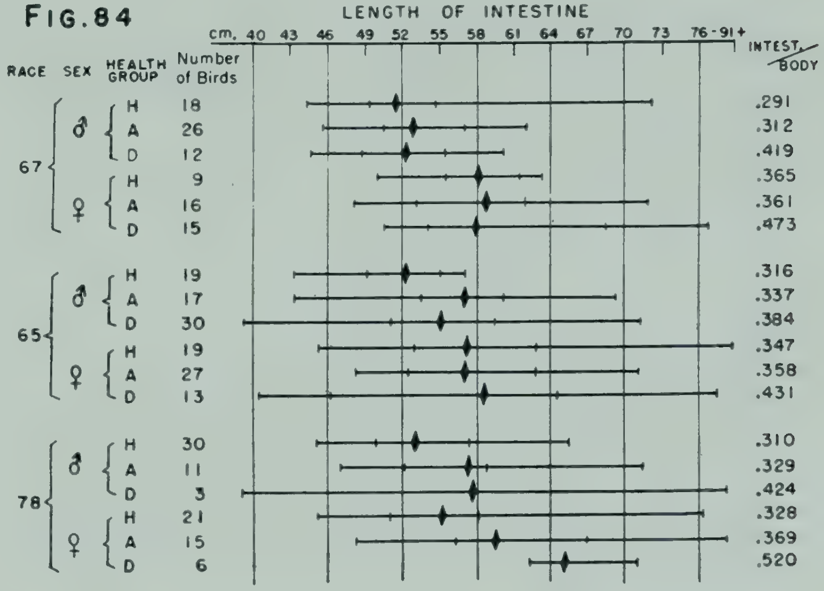


FIG. 85

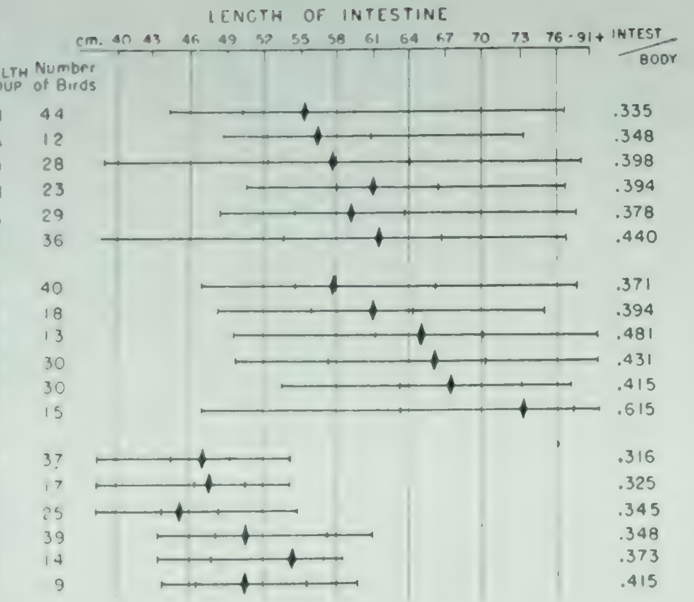


FIG. 86

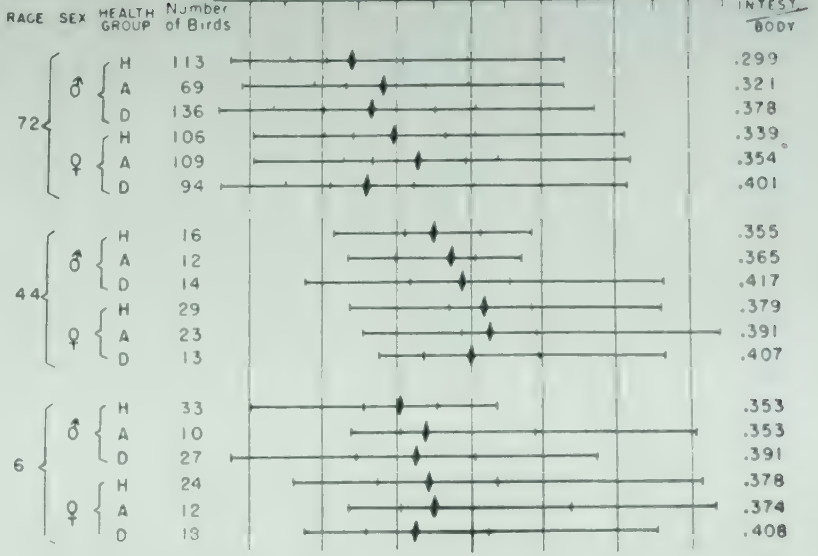


FIG. 87 LENGTH OF INTESTINE IN N2 X 62 HYBRIDS

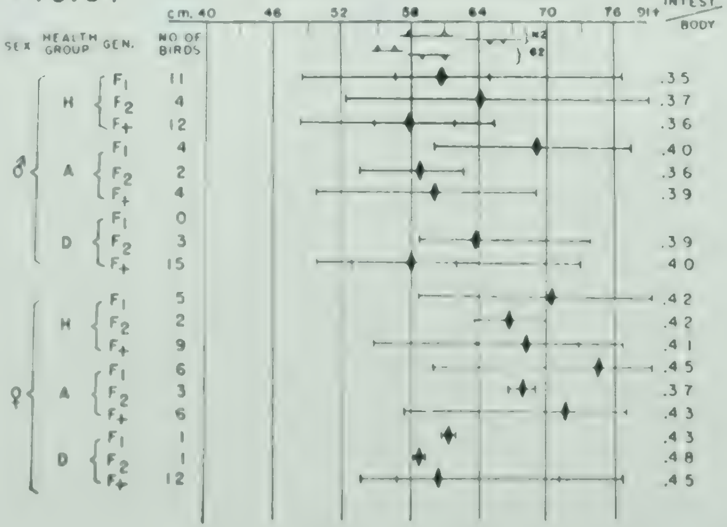


FIG. 88 LENGTH OF INTESTINE IN NA X 72 HYBRIDS

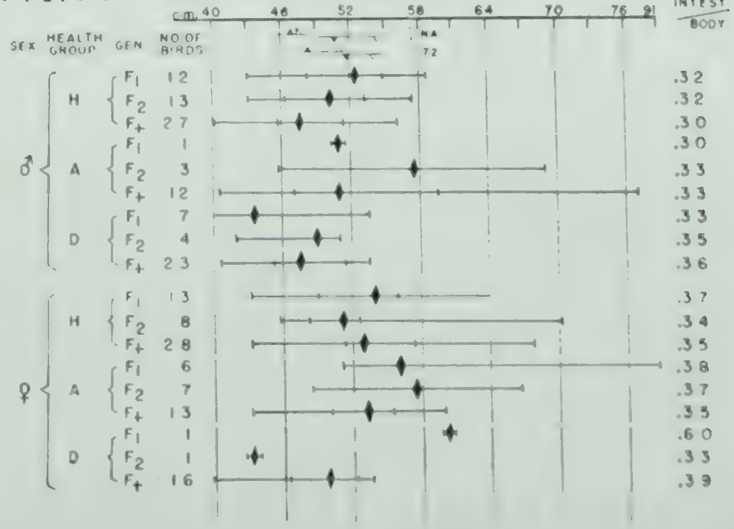


FIG. 89 LENGTH OF INTESTINE IN 36 X 72 HYBRIDS

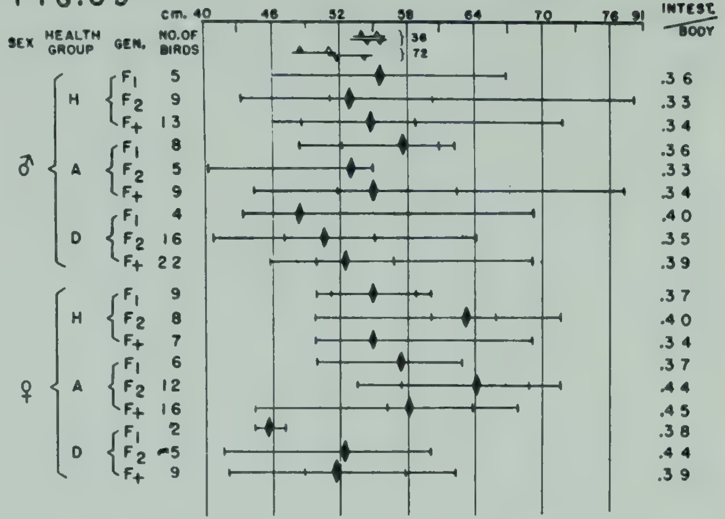


FIG. 90 LENGTH OF INTESTINE IN 62 X 63 HYBRIDS

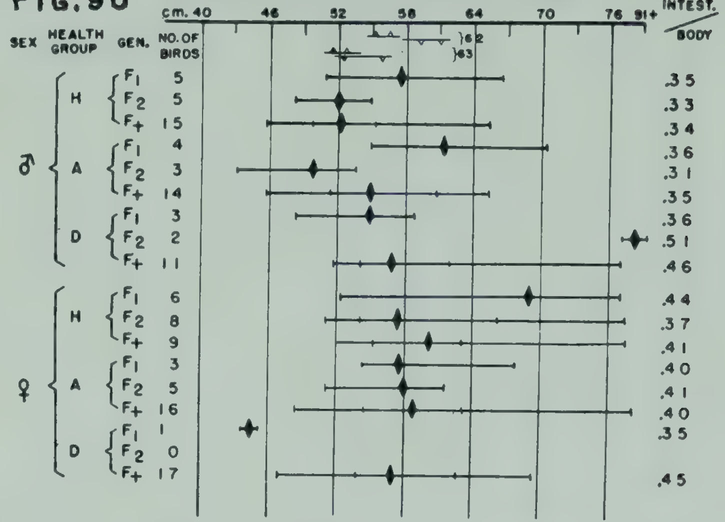


FIG. 91 LENGTH OF INTESTINE IN 36 X 62 HYBRIDS

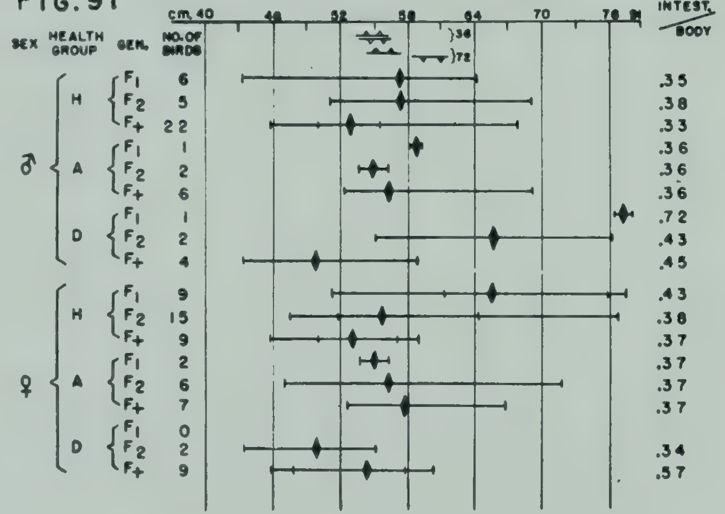


FIG. 92 LENGTH OF INTESTINE IN N2 X 44 HYBRIDS

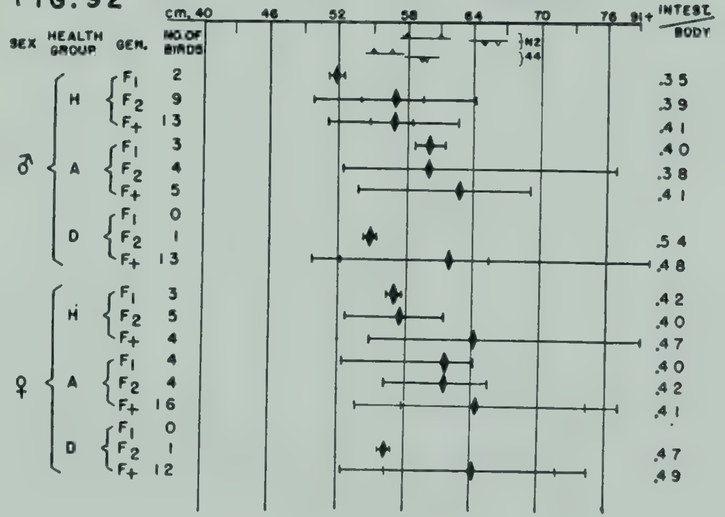


FIG. 93

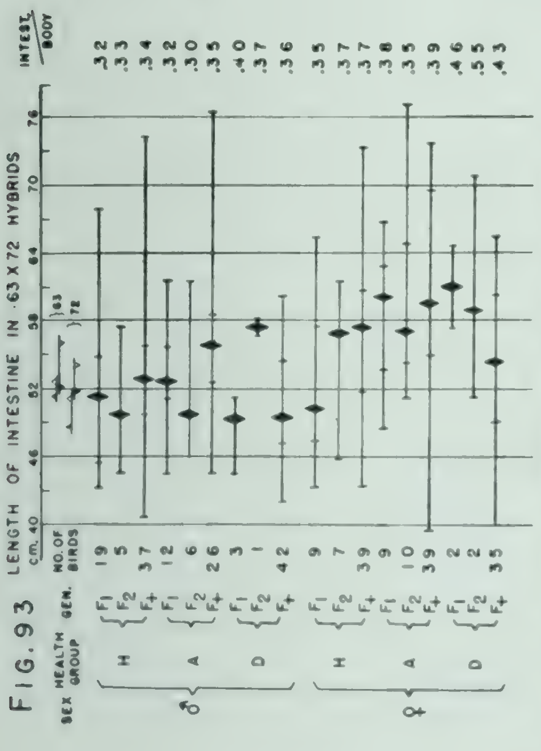


FIG. 94

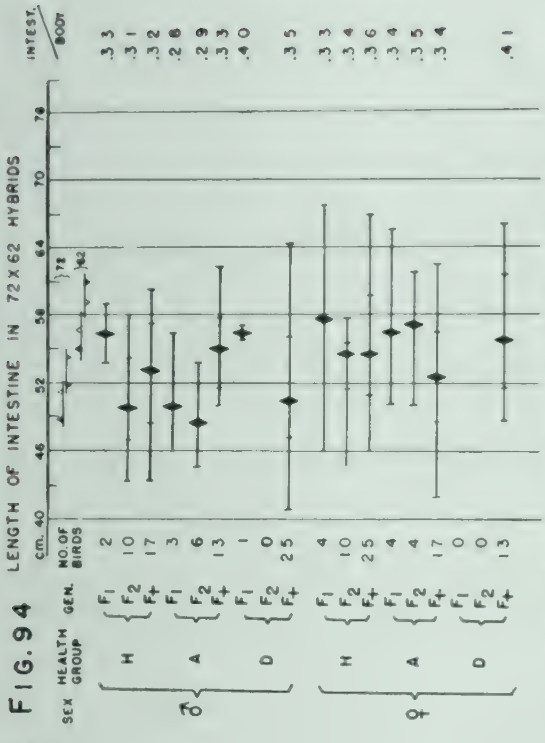


FIG. 95

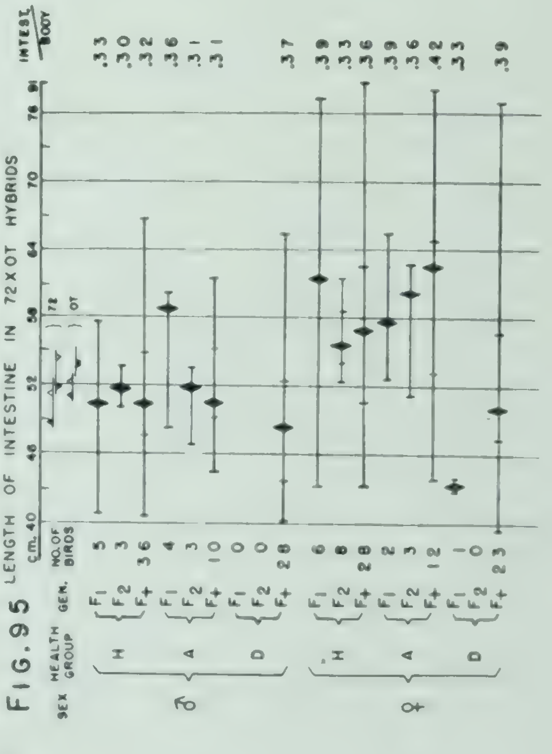


FIG. 96

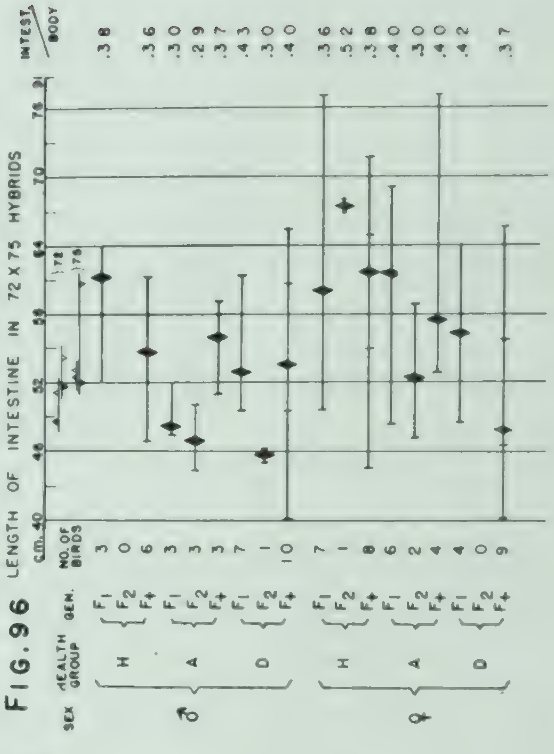


FIG. 97

LENGTH OF INTESTINE IN MINOR CROSSES

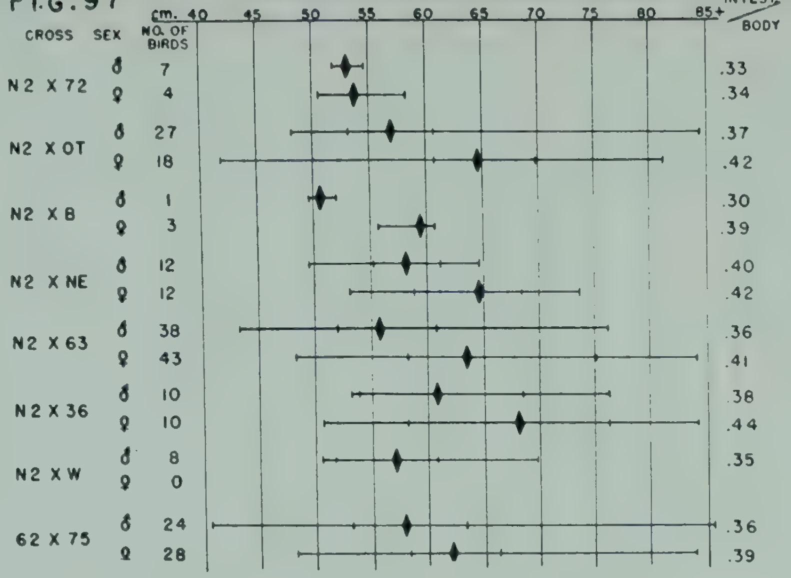


FIG. 98

LENGTH OF INTESTINE IN MINOR CROSSES

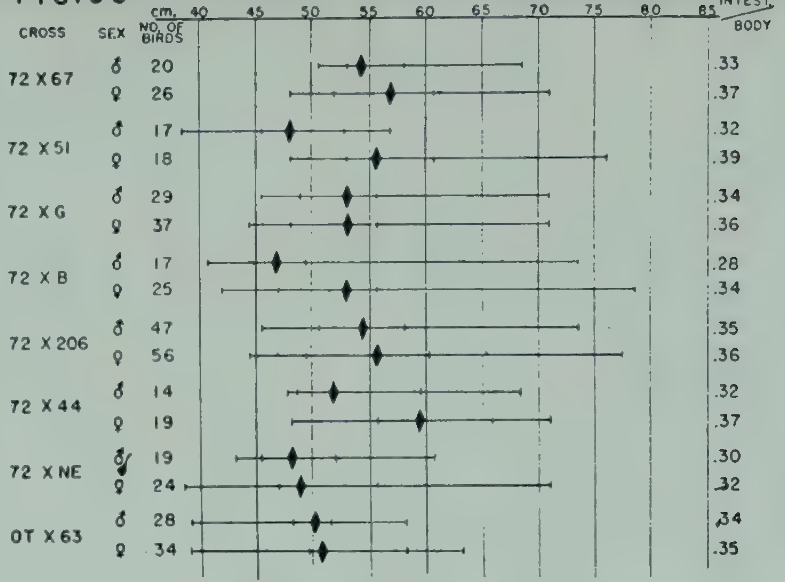


FIG. 99

LENGTH OF INTESTINE IN MINOR CROSSES

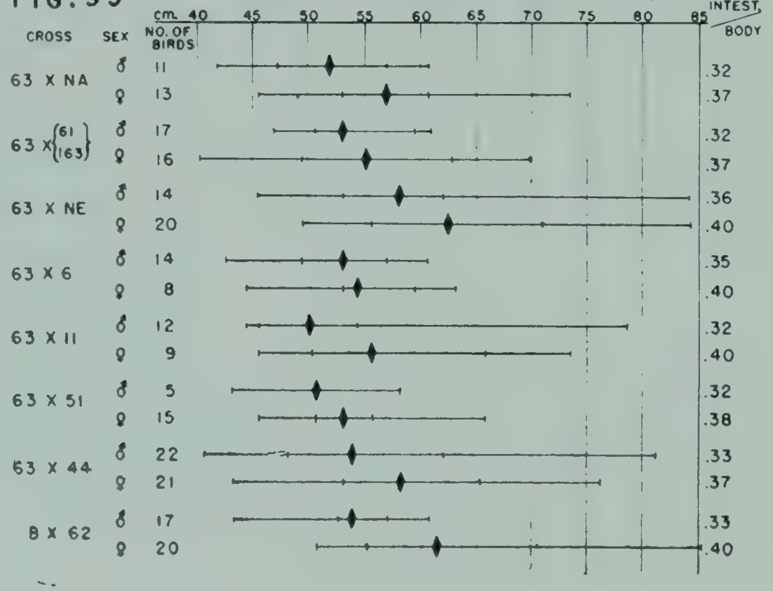
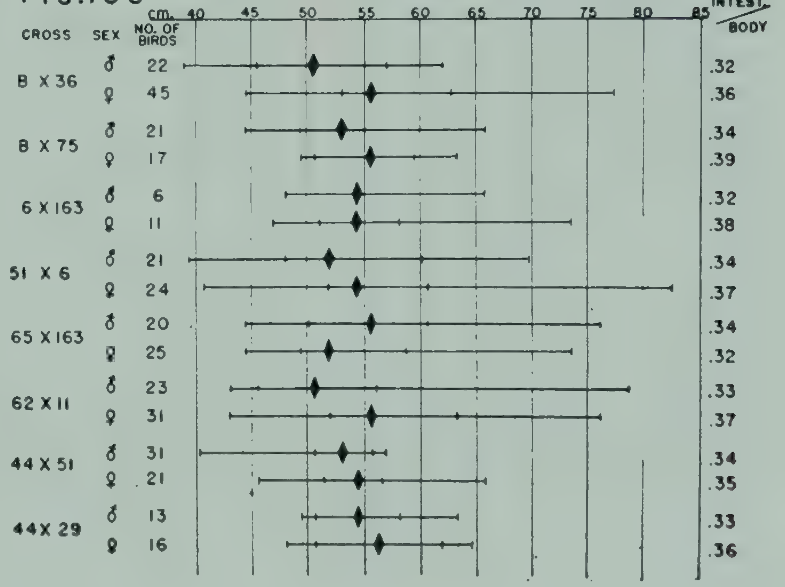


FIG. 100

LENGTH OF INTESTINE IN MINOR CROSSES



N2 (longest intestine) and *72* (shortest intestine), and these races have practically identical body weights; here actual differences in intestinal length amount to about 10 cm. for males and about 13 cm. for females, or about 20 to 25 per cent of the length in the smaller race. Differences between the other races are considerably less, especially when ratios involving body weight are considered. Usually racial differences are about equal to, or slightly smaller than, sex differences. Sex differences in actual median values range from about 2 cm. (race *75*) to about 8 cm. (race *N2*), or from about 4 per cent to about 14 per cent of the respective male values. There appears to be little or no correlation of the amount of sex difference with racial differences in body weight or intestinal length.

The correlation between intestinal length and body weight is low, even for the species as a whole, and this is especially true within each race. Data concerning ratios of intestinal length to body weight can be best examined in tabular form. Such data are provided for 18 races in table 7 and for 19 hybrid types in table 8. The values given represent the means of the two values for the two sexes. The races are listed in the order of greater length of intestine in "healthy" birds; when, on this basis, two races showed equivalent values, the data from birds with "ascariasis" determined the relative order of these races. These data provide a somewhat more accurate description of relations than was provided by the survey graph (fig. 80). The 5 races which showed greatest relative length of intestine were *N2*, *44*, *6*, *62*, and *36;* the 5 at the opposite extreme were *72*, *78*, *B*, *67*, and *OT* (the latter representing a union of races *O* and *OT*). Races *N2*, *44*, and *6* (also *63c*, soon lost) were specially selected for long intestines, and races *78*, *O*, and *NA* (also *163*, soon lost, included in *29*) for short intestines.

The fact that consistently high and low values were obtained for subdivisions (healthy and ascariasis, in both male and female) of the data for the 10 races mentioned above shows adequately that the two groups of races are genetically distinct. In general, extremes present in the early generations prevailed in the later and last generations. The attempt to establish races characterized by longer and shorter intestines was clearly successful. It should be observed that races of pure *Streptopelia risoria*, as well as those derived partly from another species, are among those found at opposite extremes.

The data from dove hybrids (table 8) show that extremes of intestinal length in parents are transmitted to their offspring (F_1 and F_2), although the number of genetic factors concerned is not established by these data. It will be observed, for example, that the 4 hybrid types which had relatively longest intestines were all derived from an *N2* parent; and that the 2 hybrid types which had relatively shortest intestines were derived from the race (*72*) with shortest intestine, the other parents (race *NA* or *OT*) also being characterized by short intestines.

One or two items of untabulated information may be noted. Hybrids of type *63* × *44* might be expected to occupy a higher place than that actually assigned to them in the table. In fact, the few F_1 individuals obtained actually show higher median values. The breeding records show that only 1 pair of F_1, and only 1 pair of F_2, were used in the propagation of this type; moreover, in both these cases

TABLE 7

Average of male and female ratios, intestinal length (in centimeters) to body weight (in grams), in three health groups of various dove races

Race	Health classes		
	Dead	Ascariasis	Healthy
N2	0.548	0.405	0.401
44	.412	.378	.367
6	.400	.364	.366
62	.419	.363	.365
36	.469	.363	.357
W	.389	.342	.353
51	.410	.346	.351
75	.464	.385	.348
63	.418	.362	.343
NE	.423	.340	.339
65	.408	.348	.332
NA	.380	.349	.332
29	.363	.347	.330
OT	.428	.338	.329
67	.446	.337	.328
B	.378	.336	.327
78	.472	.349	.319
72	0.390	0.338	0.319

the pair chosen for the continuation of the line had intestines shorter than the median for their respective fraternities. Such results may obviously be expected when the limitations of the present tests are considered, and when homozygosity in parent types was neither assumed nor established. It may be added that, although multiple factors for intestinal length apparently exist in doves, it is our opinion that fewer factors are involved than for most other characteristics examined in the present study.

Data for Pigeon Races and Hybrids

A survey of intestinal-length and body-weight relations in the two sexes of 13 breeds or types of pigeons is given in figure 101. A few dove races are included in this graph in order to show that the ratio of intestinal length to body weight is markedly lower in pigeons than in doves. Magpies (*M*) have a body weight about twice that of ordinary doves, but the length of their intestines is only about 1.5 times that of doves. Moreover, a similar alteration of ratio is seen within the former species; thus, White Kings (*WK*) have a body weight nearly double that of Magpies, but the length of their intestines is only about 1.4 that of Magpies. Though this fluctuation of the ratio somewhat complicates the comparison of

TABLE 8

Average of male and female ratios, intestinal length (in centimeters) to body weight (in grams), in hybrid doves

Cross	F_1	F_2 and F_+	
		Ascariasis	Healthy
N2 × OT	0.369	0.391	0.436
N2 × 44	.392	.405	.418
N2 × 62	.405	.388	.390
N2 × 63	.395	.392	.387
62 × 75	.364	.381	.375
72 × 75	.380	.340	.370
OT × 63	.361	.346	.367
72 × 206	.339	.375	.362
36 × 62	.378	.365	.365
62 × 63	.383	.363	.363
44 × 51	.334	.358	.361
51 × 6	.369	.391	.356
36 × 72	.365	.390	.353
63 × 72	.343	.348	.353
B × 36	.355	.385	.341
72 × 62	.320	.328	.333
63 × 44	.392*	.343	.330
72 × OT	.368	.350	.328
NA × 72	0.343	0.345	0.328

*Data from only 7 birds.

races, it is fairly evident that Homers *C* (*HC*) and Tipplers (*T*) have intestines somewhat shorter than the trend, whereas Carneaux (*C*) and *SA-R* (scraggly) have intestines longer than the trend. It should be noted that extra length of intestines in scraggly *SA-R* (and *SA-E*) is probably the result of extra food consumption rather than a direct effect of the gene for scraggliness. This gene prevents the formation of plumage with usual heat-conserving properties; excess heat loss (and heat production; see part II) compels extra food consumption, and the latter has earlier been noted[13] to lengthen the intestines of immature pigeons. Thus, in scragglies, an environmental condition probably has an especially marked effect on intestinal length; in the scragglies of one group (*SA-E*) this increase is about 10 per cent, and in the other (*SA-R*) it is nearly 13 per cent. In all the other races listed, intestinal length may be presumed to be somewhat more definitely under genetic and endocrine control.

Both the graph and the percentile analyses (figs. 102–114) indicate that median intestinal length, in relation to body weight, was usually less in males than in

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[13] See footnote 11.

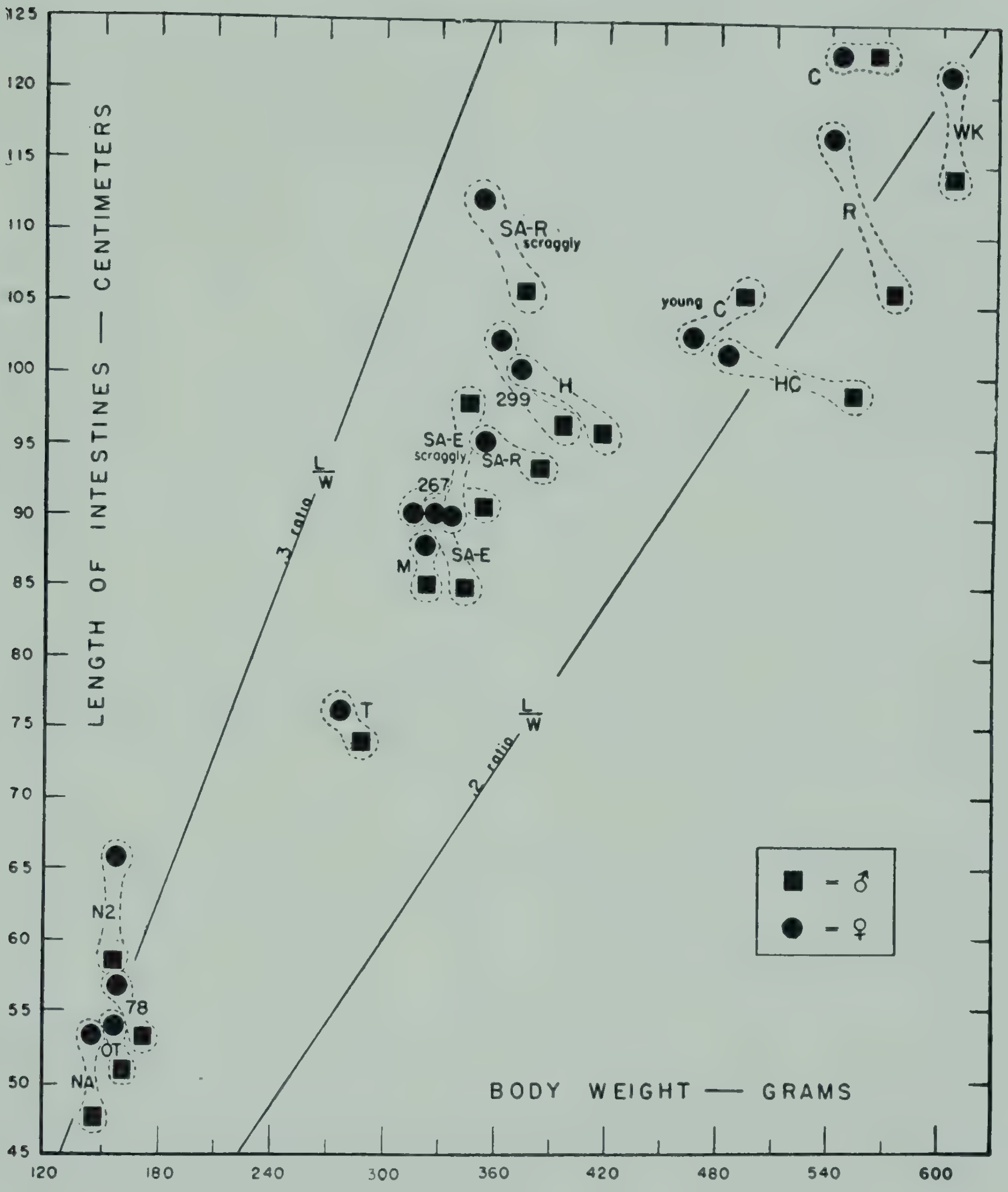

FIG. 101. A survey of both intestinal length and body weight in the two sexes of various races of pigeons. For comparison, similar values are provided (at lower left of graph) for 4 dove races. The data were obtained from healthy adults, including those with intestinal parasites (ascariasis).

females. Scraggly *SA-E* may be a real exception, but young Carneau (*C*) probably is not. The latter birds were not reared in our own colony; and slight differences in age, in these quite immature birds, probably affected the values obtained.[14] In general, sex difference in intestinal length is less marked and less constant in pigeons than in doves.

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[14] See footnote 10.

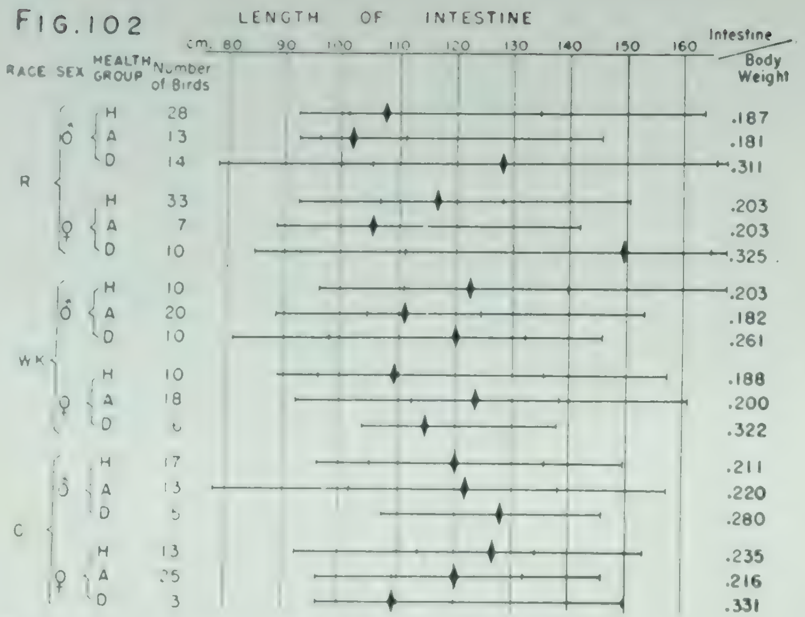


FIG. 102

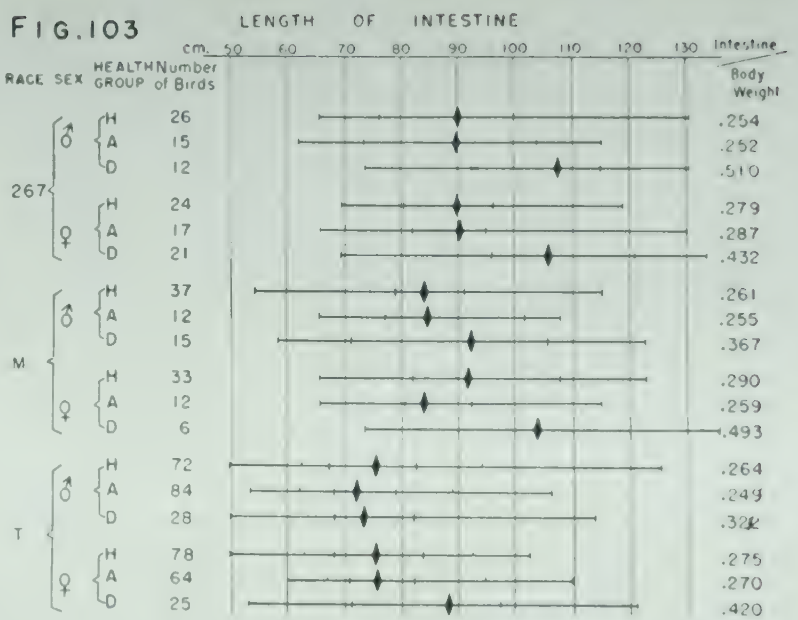


FIG. 103

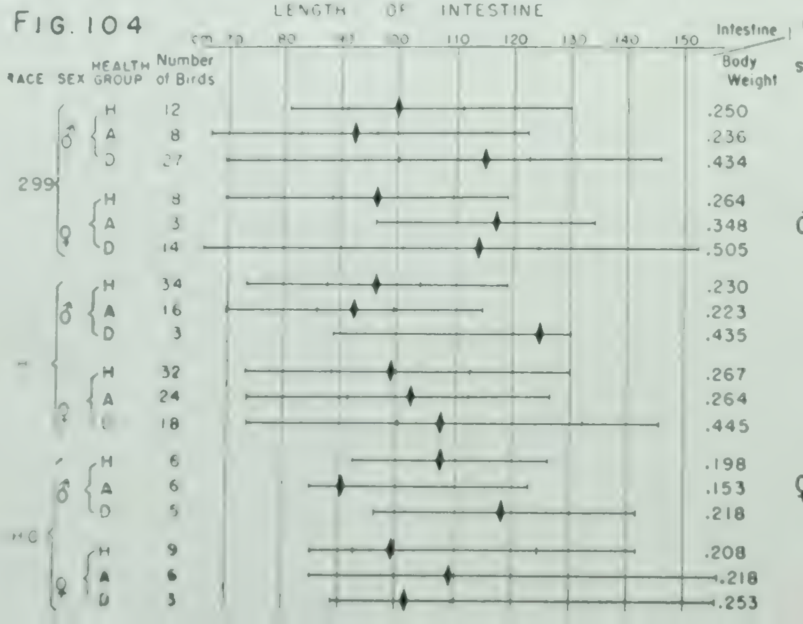


FIG. 104

INTESTINAL LENGTHS, EARLY SCRAGGLY-ATAXIC (Mixed) STOCK (1922-27)

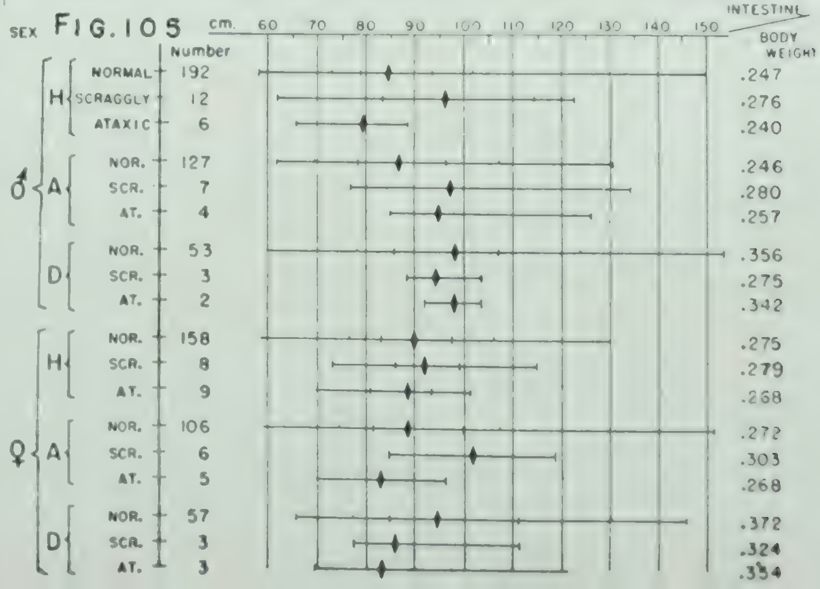


FIG. 105

FIG.106

MAGPIE X TIPPLER
LENGTH OF INTESTINE

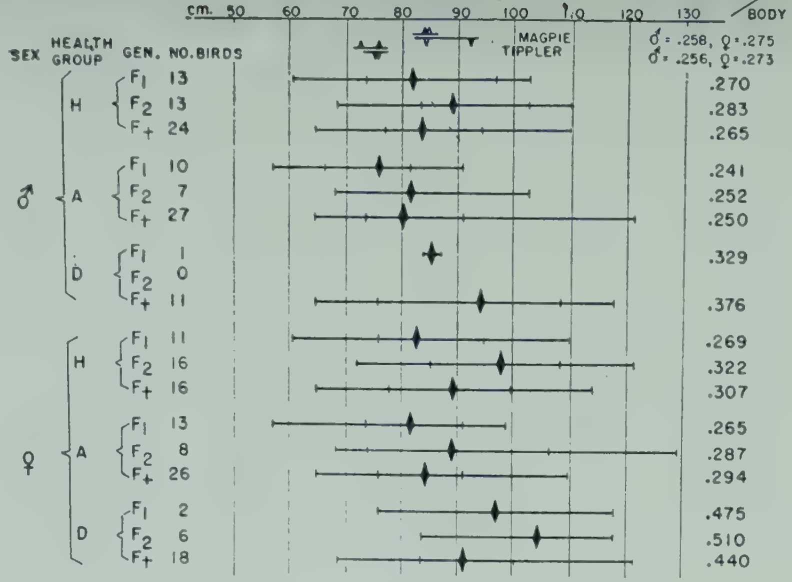


FIG.107

TIPPLER X 267
LENGTH OF INTESTINE

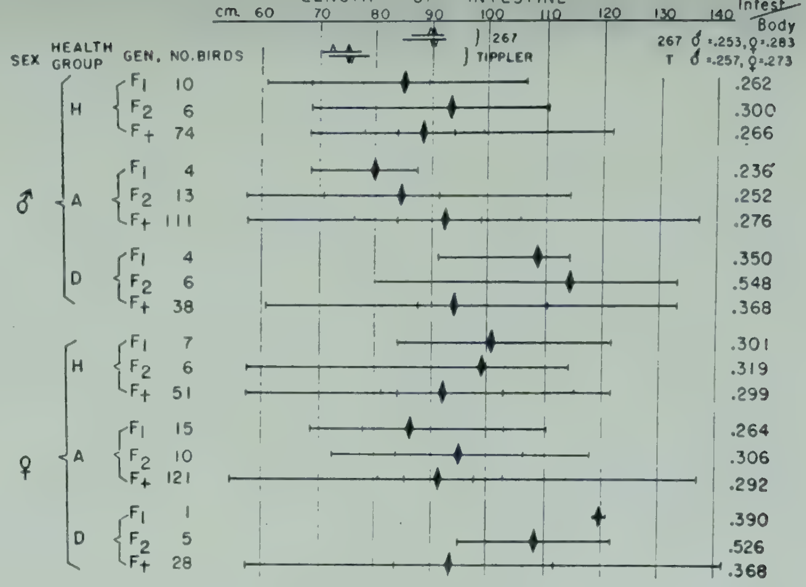


FIG.108

HYBRIDS, TIPPLER X SA-E
LENGTH OF INTESTINE

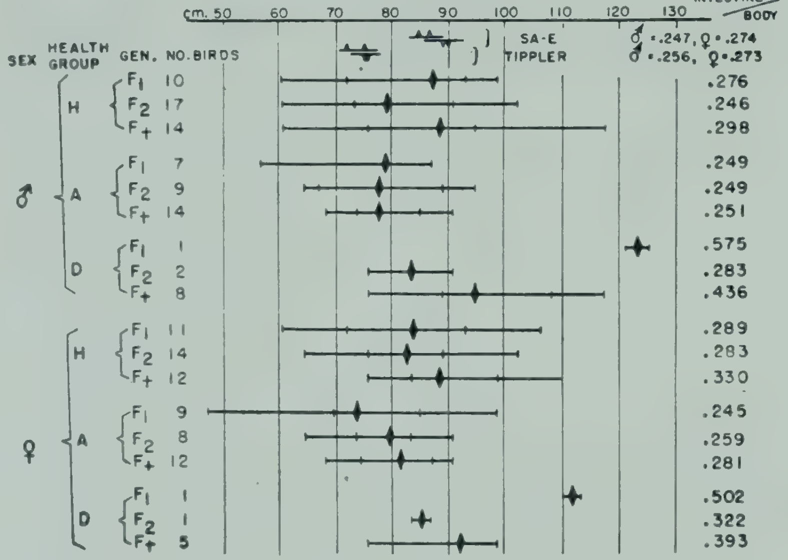


FIG.109

HOMER X TIPPLER
LENGTH OF INTESTINE

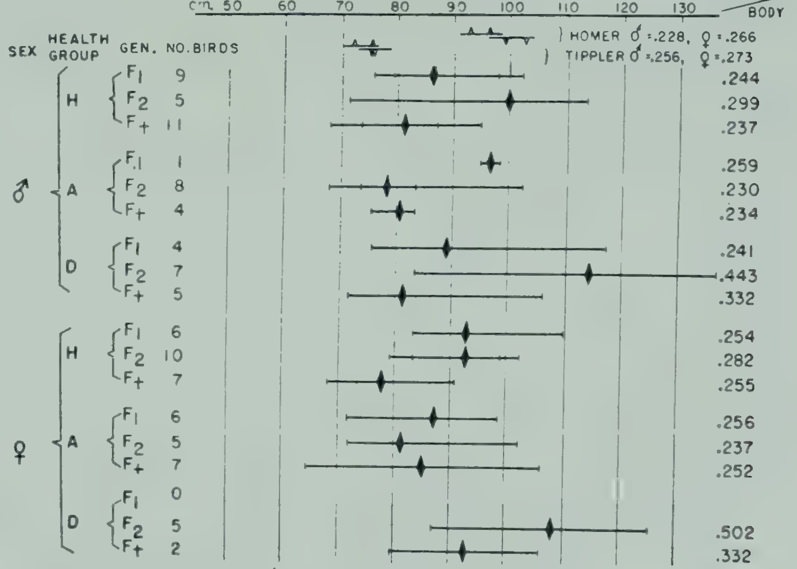


FIG.110

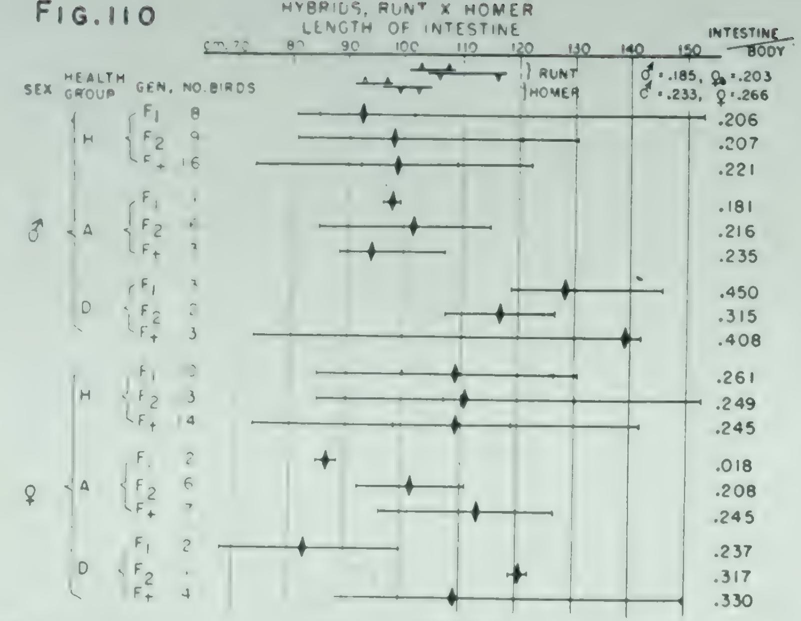


FIG.111

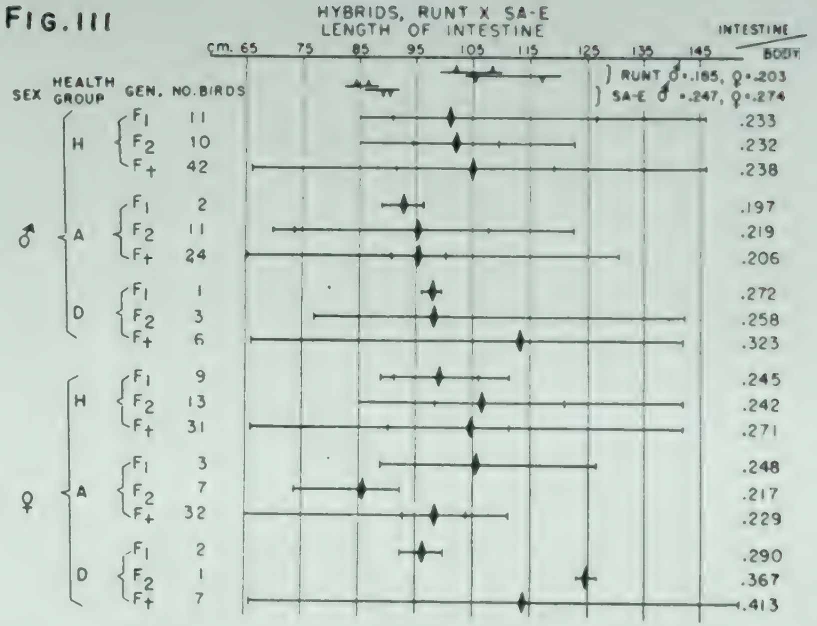


FIG.112

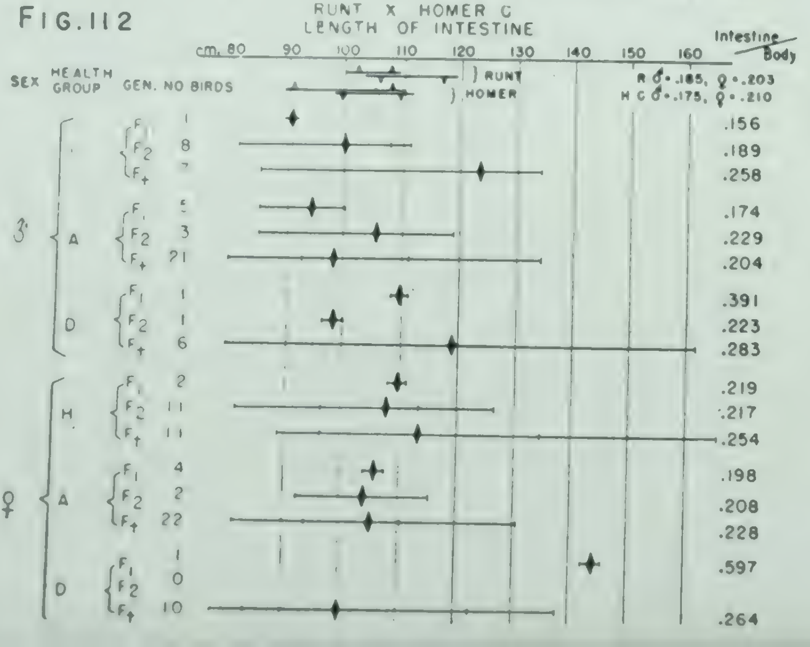


FIG.113

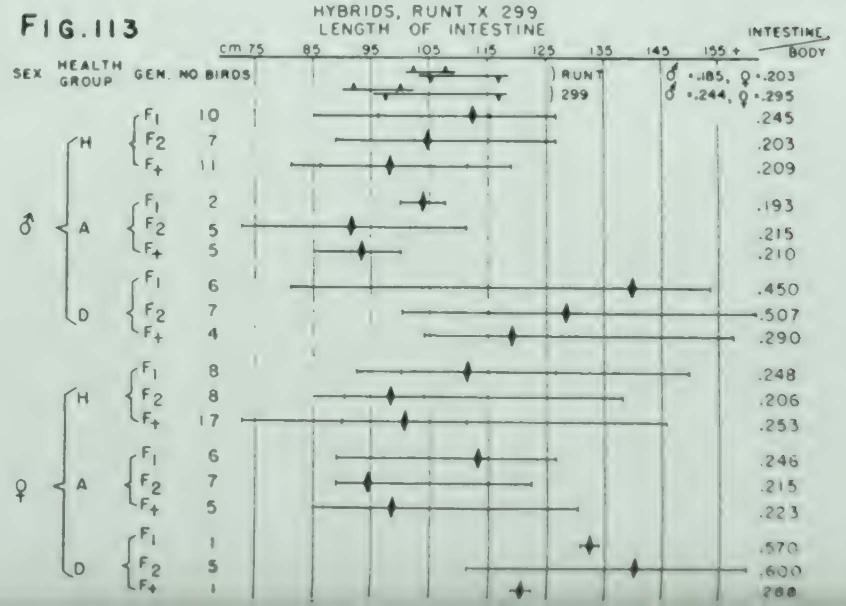
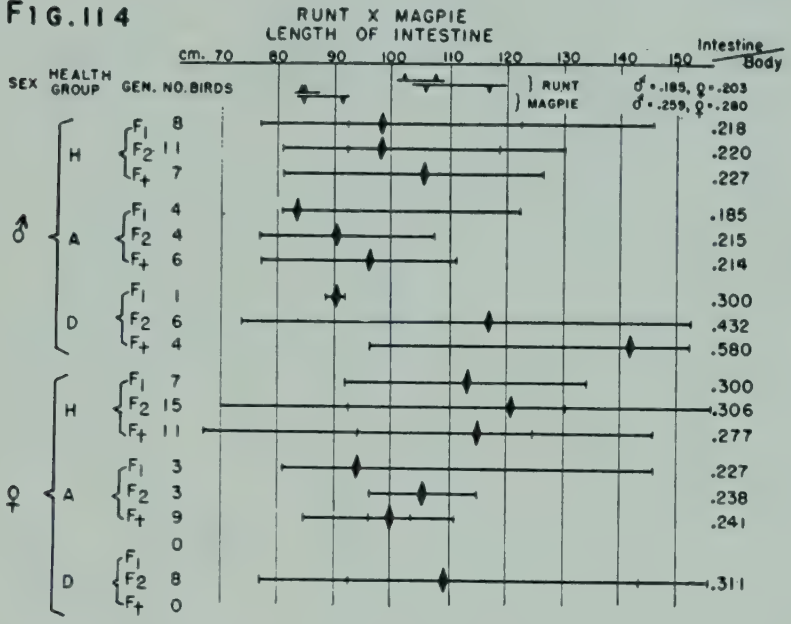


FIG. 114



The percentile analyses show that ascariasis had no consistent effect on intestinal length in pigeons; other diseases, however, had a more marked tendency to increase intestinal length in pigeons (except scragglies; fig. 105) than in doves. Coefficients of dispersion are slightly larger in data for pigeons than in those for doves; the smallest is about 0.06 for Homer males, and the largest (scragglies excluded) is about 0.14 for males of race 267.

Partly because changing body weight involves a change in the ratio between intestinal length and body weight, the data from hybrids do not provide satisfactory information for analysis of genetic factors for intestinal length. In general, the values from hybrids tend to be intermediate to values for the parental races, and thus to indicate "blending inheritance."

PITUITARY SIZE IN ITS RELATION TO RACE, SEX, AND INTESTINAL LENGTH

It was stated above that the selection of birds with extremes of intestinal length was practiced primarily to assure the establishment of some races with larger and others with smaller pituitary glands. It is further to be noted, however, that 16 additional (unselected) pairs of doves were chosen as founders of races, and that reproductive performance (or thyroid size) was there the basis of choice and selection. Much interest attaches therefore to any available evidence concerning pituitary size in these 24 races. Were "pituitary races" established? And what relation exists between pituitary size and intestinal length? During 1932–1933 the weights of a few hundred pituitary glands were obtained, and these data are given in tables 9 and 10. The birds used in this study were removed by three to seven generations from the starting point of the race or cross. It was expected that a second series of similar measurements would be made at or near the end of this study (1940–1944), but wartime conditions prevented fulfillment of that plan.

TABLE 9

AVERAGE INTESTINAL LENGTHS AND PITUITARY WEIGHTS IN MALES AND FEMALES OF VARIOUS RACES OF RING DOVES

Race or cross	No. of cases	Intestinal length (cm.)	Body weight (gm.)	Ratio, intestinal length to body weight	Weight of pituitary (mg.)		Ratio, whole pituitary to body weight	Ratio, anterior lobe to body weight
					Whole gland	Anterior lobe		
62+..........	♂19	56.4	159.5	0.354	2.03	1.64	127*	102*
	♀15	54.3	151.2	0.359	2.00	1.61	132	106
36 × 62.......	♂19	55.1	157.8	0.349	2.04	1.66	129	105
	♀11	54.3	151.9	0.358	2.14	1.75	141	115
6+...........	♂14	53.3	154.4	0.345	2.11	1.69	136	109
	♀10	57.2	154.6	0.370	2.66	2.17	172	140
N2+.........	♂15	57.9	148.1	0.391	2.05	1.70	137	115
	♀ 9	67.0	152.7	0.439	2.22	1.83	145	120
72 × 63+.....	♂10	53.8	168.9	0.318	2.14	1.80	127	106
	♀12	55.3	158.3	0.349	2.17	1.84	137	116
72 × 62.......	♂10	53.1	168.8	0.315	2.37	1.94	140	115
	♀ 9	54.1	152.8	0.354	2.54	2.12	166	139
72+..........	♂10	51.1	166.9	0.306	2.42	2.00	145	120
	♀ 9	56.9	155.0	0.367	2.66	2.26	171	146
63 × 6+......	♂ 9	50.3	156.1	0.322	2.11	1.69	135	108
	♀ 9	55.6	149.1	0.373	2.09	1.69	140	113
OT × O......	♂ 9	51.3	153.3	0.335	2.03	1.63	133	106
	♀ 8	54.1	155.5	0.348	2.19	1.76	141	113
NA × 72......	♂ 8	48.3	153.8	0.314	2.01	1.68	131	109
	♀ 9	49.1	150.6	0.326	2.28	1.86	151	123
B+...........	♂10	46.2	154.5	0.299	2.18	1.85	141	120
	♀ 7	53.8	157.0	0.343	2.50	2.16	159	137
75............	♂ 6	57.2	152.7	0.375	2.35	1.95	154	128
	♀ 8	58.2	135.3	0.430	2.36	1.99	175	147
51............	♂ 8	49.8	153.0	0.325	1.83	1.50	120	98
	♀ 6	54.6	152.0	0.359	1.72	1.33	113	88
75 × B.......	♂ 5	52.3	158.4	0.330	2.06	1.66	130	105
	♀ 3	50.1	150.7	0.332	2.37	2.00	151	133
Misc..........	♂15	55.3	161.9	0.342	2.24	1.85	139	114
	♀13	56.2	155.4	0.362	2.25	1.83	145	118
Mean.......	♂(15)	52.8	157.9	0.335	2.13	1.75	135	111
Mean.......	♀(15)	55.4	152.1	0.365	2.27	1.88	149	124

*Written out fully, these figures are 0.0000127, 0.0000102, etc.

TABLE 10

AVERAGE INTESTINAL LENGTHS AND PITUITARY WEIGHTS IN MALES AND FEMALES OF VARIOUS RACES OF COMMON PIGEONS

Race or cross	No. of cases	Intestinal length (cm.)	Body weight (gm.)	Ratio, intestinal length to body weight	Weight of pituitary (mg.)		Ratio, whole pituitary to body weight	Ratio, anterior lobe to body weight
					Whole gland	Anterior lobe		
M × T.......	♂16	83.3	316.4	0.263	4.55	3.74	144*	118*
	♀25	86.4	292.0	0.296	4.75	4.01	163	137
T × 267......	♂10	93.5	331.7	0.282	4.51	3.76	136	113
	♀16	93.7	299.5	0.313	4.79	3.98	160	132
T × 133......	♂15	82.8	304.6	0.272	4.49	3.82	147	125
	♀13	87.9	293.2	0.300	4.40	3.76	150	128
R × 133......	♂12	102.4	453.3	0.226	5.89	5.18	130	114
	♀13	95.3	391.7	0.243	5.59	4.93	143	126
T.............	♂10	72.4	265.2	0.273	3.99	3.30	150	124
	♀11	76.7	255.1	0.301	4.35	3.60	170	141
SA-R.........	♂ 8	104.4	387.9	0.269	5.25	4.46	135	115
	♀ 9	109.7	347.0	0.316	5.16	4.44	148	128
H............	♂ 5	97.0	425.2	0.228	6.16	5.26	145	124
	♀ 7	98.8	436.0	0.227	6.21	5.54	142	127
H × T........	♂ 6	94.7	350.0	0.271	4.52	3.70	129	106
	♀ 6	84.8	310.8	0.273	5.00	4.30	161	138
M × 267......	♂ 4	96.0	367.8	0.261	5.23	4.55	142	124
	♀ 7	100.1	305.6	0.328	5.43	4.67	178	153
133 × 267.....	♂ 5	83.6	366.6	0.228	4.70	4.12	128	112
	♀ 5	94.0	348.3	0.270	5.16	4.54	148	130
PT × 272.....	♂ 6	88.3	314.0	0.281	5.12	4.50	163	143
	♀ 3	95.3	299.0	0.319	4.80	4.33	161	145
M............	♂ 5	82.8	328.4	0.252	5.44	4.62	166	141
	♀ 3	87.2	295.7	0.295	6.10	5.27	206	178
267 × H......	♂ 4	85.8	403.0	0.213	5.23	4.50	130	112
	♀ 3	98.3	356.0	0.276	5.77	5.13	162	144
Mean.......	♂(13)	89.8	354.9	0.255	5.01	4.27	142	121
Mean.......	♀(13)	92.9	325.4	0.289	5.19	4.50	161	139

*Written out fully, these figures are 0.0000144, 0.0000118, etc.

Details concerning these data are given elsewhere,[15] and only a brief statement is required here. Most of the tabulated material was from healthy birds aged 5 to 36 months, but about 10 per cent of it was from somewhat younger birds which yielded values apparently similar to those obtained from related adults. A plus (+) sign following the name of a race indicates that comparable data from a few hybrids are included with data for the parental race.

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[15] See footnote 5.

The data of table 9 indicate that race 5*1* had the smallest pituitary glands found in measurements made on 7 races and 8 hybrid types. All the four averages for race 5*1*, from the four separate weighings (whole gland and anterior lobe only, in both sexes), differ from the mean for all other types by a value which is equal to or greater than the error involved in the weighing of a single gland. The same method of reckoning indicates that races 75 and 72 had pituitaries significantly heavier than the mean value found for the other types. It should be noted at once that the particular individuals of race 75 which were used in this measurement, and whose pituitaries were absolutely and relatively the heaviest, also had intestines of greater absolute and relative length (both sexes) than any other group except race *N*2. In individuals of the latter race (*N*2), however, absolute and relative pituitary size (both sexes) was indistinguishable from the mean obtained for the 15 racial types. Again, those individuals of race 5*1* which were found to have the smallest pituitaries had intestines whose length (relative to body weight) was practically the same as the mean obtained from all types. Furthermore, in race 72, whose pituitaries were rather large, the intestines of males were unusually short, whereas those of females had a length equivalent to the mean value obtained for the several types. Within related populations (races) of doves, therefore, it seems that an extreme of pituitary size may be associated, but more often it is not associated, with a corresponding extreme of intestinal length.

When sex, not race, is made the basis of comparison, the data of table 9 clearly show that the female sex has both a heavier pituitary and a longer intestine. The ratios involved show heavier female pituitaries in 14 of the 15 types, and longer intestines in all the 15 types. Since, in the case of several types, too few individuals were used to provide really accurate measurements, a confirmation of this result is desirable. This confirmation is found in the fact that a quite comparable result was obtained (table 10) from measurements made on 13 types of pigeons.

Relative pituitary size does not seem to be clearly associated either with body weight or with thyroid size in either dove or pigeon races. It may be remarked, however, that race 75, which is here found to have pituitaries of extreme size in relation to body weight, is elsewhere found to have the smallest thyroids and the highest basal metabolic rate encountered among a still larger number of dove types. Again, race 5*1*, with extremely small pituitaries, carried genes for myoclonus, had a body temperature (40.8° C.) about 1° C. lower than that of other races,[16] had rather small thyroids, and had a rather high metabolic rate.

Table 10 gives data for 5 pigeon races (*T* × *267* = "hermaphrodite-producing race") and 8 types of hybrids. Very few measurements were made on several breeds and types. Anterior lobes in relation to body weight were larger in females than in males in all the 13 types; the absolute weight of the glands was greater in the females of 9 types. Body weight was greater in the males of all types except Homers (*H*); the body weight of female Homers used in these tests appreciably exceeded the average for the breed (see fig. 101). Intestinal length was absolutely greater in the females of 11 types, and it was relatively greater in all types except Homers. It is evident therefore that, as in doves, the sex which has the larger anterior lobes (and whole pituitaries) is also the sex which has the longer intestines.

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[16] Riddle, O., G. C. Christman, and F. G. Benedict, Amer. Jour. Physiol., 1930, vol. 95, p. 111.

Relatively largest whole pituitaries and anterior lobes (both sexes) were obtained from Magpies. Relative intestinal length in this breed (i.e., in the specimens used) was indistinguishable from the mean value for the several types; but, like the comparable group (race *75*) among the doves, the Magpies had a higher basal metabolic rate than any other type of pigeon (except scragglies). The males only of another type (*PT* × *272*, a subdivision of *SA-E*) had whole pituitaries and anterior lobes which were significantly larger than the mean for all types; relative intestinal length in these males was as usual or expected for birds of rather low body weight. Relatively smallest pituitaries were found, apparently, in types *R* × *133*,[17] *133* × *267*, and *SA-R*. These types had body weights exceeding those of nearly all other types, and their relative intestinal lengths (except in *SA-R*) were quite normal for pigeons of their body weight; in race *SA-R* both absolute and relative intestinal length (both sexes) exceeded the mean value obtained for all types.

The data just presented make it fairly evident that, within the breeds of pigeons, relatively large pituitaries are not associated with long intestines or with large body size. Relative pituitary size does appear to differ, however, in the different racial types. Moreover, both whole pituitary and anterior lobe show a well defined tendency (in both sexes) to be relatively heavier in the large breeds of pigeons than in the much smaller races of doves. In relation to body weight, the intestines of large breeds of pigeons are definitely shorter than those of the much smaller races of doves.

Conclusions and Summary

An attempt was made to select and segregate strains (races) characterized by longer and shorter intestines from a population of ring doves whose grades of mongrelization were apparently comparable with those present in the human population of an American city. Data showing that that effort was successful are recorded here.

It was initially thought probable that selection of unusually long intestines would prove to be a practicable method, and give additional assurance, of obtaining dove races with unusually large pituitary glands; also, that short intestines might prove to be associated with small pituitary glands.

An early study of actual and relative pituitary size in a few dove races and hybrids indicated that, on a basis of race, there was no close or constant relation of pituitary size to intestinal length, body weight, or thyroid size (see table 68 and chapter 18). Relatively largest pituitaries were found, however, in the type (race 75) with smallest thyroid size, highest metabolic rate (the latter duplicated in the pigeon breeds studied), and, in the sample of birds used, unusually long intestines. Another population (race 72) with relatively large pituitaries had large thyroids and short intestines. The population (race *51*) with smallest pituitaries had intestines of medium length; this race carried recessive genetic factors for myoclonus, and its members had a body temperature about 1° C. lower than that of other doves. Relatively larger pituitaries and relatively longer intestines, however, are found in the females of practically all races and types.

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[17] Group *133* was a subdivision of *SA-E*.

A similar examination of pituitary size in a few pigeon breeds gave essentially similar results. Magpies, a "tall" type of pigeon showing maximum rate of heat production, had the largest whole pituitaries and anterior lobes. Both whole pituitary glands and anterior lobes showed a well defined tendency to be relatively heavier in the large breeds of pigeons (whose intestines are relatively shorter) than in the much smaller races of doves. On the basis of pituitary weights obtained (near the end of the first half of the present study) on 305 healthy doves and 227 healthy pigeons, some races characterized by larger and smaller pituitary glands were apparently established. Further evidence on this point should have been obtained in both doves and pigeons at or near the end of this investigation, but that study was not undertaken.

Ascariasis is usually accompanied by a small increase in intestinal length in ring doves. Dead and diseased doves usually showed no actual increase in intestinal length.

Intestinal length is relatively greater, and usually it is also absolutely greater, in females than in males, although body weight is nearly always less in the females. The two races (*N2* and *44*) which had most extreme intestinal length did not show the usual sex difference in body weight.

Twenty-four pairs of doves were selected from more than 200 pairs whose ancestry and reproductive records were largely known; a few pairs were closely related or their progeny soon died, but from 18 of these pairs significant data for intestinal length in several generations were obtained.

Races *N2*, *44*, *6*, *62*, and *36* were characterized by unusually long, though not equally long, intestines. Races 72, 78, *B*, *67*, *OT* (including *O*), *29*, and *NA* were characterized by short, though not equally short, intestines. In races *W*, *51*, 75, and *63* the intestines were of "intermediate" length. The extremes of intestinal length persisted from early through later generations. Both extremes of intestinal length include races derived from pure *Streptopelia risoria*, and also other races containing an admixture of another species or genus.

Thirteen dove races were used one or more times in crosses which produced 19 types of hybrids. Data from these crosses show that both extremes of intestinal length are inherited, though the nature and number (more than one, but probably not many) of genetic factors involved was not established.

In long-established pigeon breeds, and in newer breeds and hybrids of pigeons, intestinal length is relatively greater in females than in males. Despite irregularities associated with differences in body weight, there is evidence that the intestines of Homers *C* and Tipplers are shorter, and those of Carneaux are longer, than those of some other breeds of corresponding body weight.

The sex difference in intestinal length in pigeons is less than that observed in doves; the ratio of intestinal length to body weight is less in pigeons than in doves and less in large breeds than in small breeds of pigeons. Ascariasis affects intestinal length in pigeons less, and less consistently, than in doves. On the other hand, intestinal length tended to be markedly increased in dead and diseased pigeons, but not in dead and diseased doves.

6

LIVER SIZE IN A STUDY OF RACES

Both liver function and liver weight fluctuate under the influence of a number of hormones. Such changes are doubtless to be expected in an organ which performs several functions of much importance to the remainder of the organism. But these fluctuations also occur, or now appear to occur, in some or several diseases in which endocrine glands are little if at all involved. Such diseases, particularly if unrecognized, are therefore probably capable of masking those changes in liver weight which are mediated by hormones. Despite these uncertainties, and at the outset of this study, it was considered important to make careful records of liver weight in every animal for two reasons: first, to have the evidence of liver weight on the question of the diseased or healthy state of the individual; and, second, to have, at the end of the racial study, data from healthy livers which might show instructive correlations with such measurements as intestinal length, thyroid weight, age at maturity, etc.

In the years which followed, certain studies were conducted in this laboratory on factors concerned in change in liver weight in doves and pigeons. The results of these studies have shown, for example, that liver weight varies somewhat with sex, with season, and with stages within the egg-laying or reproductive cycle. These particular changes, and perhaps some others to be noted later, are in part probably peculiar to birds or at least to egg-laying vertebrates. Liver weight did not appear to vary with sex in rats.[1] In some measure, therefore, the present data concerning liver weight are best compared with data from a similar series of races or breeds of other birds. It is unfortunate that very few such data are as yet available.

THE ROLE OF ENDOCRINE FACTORS IN LIVER-WEIGHT CHANGES IN DOVES AND PIGEONS

The role of sex and season was investigated[2] in 499 male and 444 female ring doves, all apparently healthy, and aged 6 to 30 months (adults). Though body weight was 2 per cent greater in the males, their livers averaged 9.4 per cent smaller than those of the females. During spring and summer, liver weight increased over autumn and winter values by 10.4 per cent (male) and 6.1 per cent (females). It was observed that these seasonal changes were positively correlated with size changes in testis and ovary, and negatively correlated with size changes in the thyroids of these animals. The spleen showed sex and seasonal variations wholly comparable with those observed in the liver. A part of the present material was utilized in the study just described.

[1] Donaldson, H. H., The rat (Mem. of Wistar Inst. of Anat. and Biol., no. 6, Philadelphia, 1924).

[2] Riddle, O., Proc. Soc. Exper. Biol. and Med., 1928, vol. 25, p. 474.

In a relatively small group of pigeons killed at the several stages of the reproductive cycle, Schooley and Riddle[3] observed an apparent increase (13 to 15 per cent) in liver weight during incubation of eggs and during the feeding of young. Though there is some doubt concerning the accuracy and adequacy of these measurements, there is no doubt that at the two periods indicated a greater amount of prolactin was being released from the pituitaries of the birds whose livers were apparently enlarged.

Specific ability of the anterior pituitary hormone prolactin to increase liver weight (also body weight, and *intestinal* length and weight) has been clearly indicated.[4] Four daily injections of prolactin (total, 20 mg.) increased liver weight of young (2.2 months) Carneau pigeons from 9.7 ± 0.4 gm. to 16.4 ± 0.9 gm. This represents an increase of 67 per cent in liver weight while body weight was increased by less than 17 per cent. Another study[5] showed that prolactin induced a similar increase in liver weight in young Carneau pigeons whose pituitary glands had been removed; in this case, however, by far the greater part of the increase was prevented if these birds were completely fasted during the 10-day period of prolactin injections. In a still later study[6] on hypophysectomized pigeons it was found that liver weight was sustained both by prolactin and by hormones of the adrenal cortex; and, further, that addition of small doses (5 or 10 gammas daily) of thyroxin to such treatments tended to diminish the ability of those hormones to increase liver weight.

Lee and Freeman[7] showed that an extract of anterior pituitary tissue produced a true hyperplasia, involving relatively greater increase in liver weight than in body weight, in normal rats. Their extract was regarded as "growth hormone," but it seems entirely probable that it contained effective amounts of prolactin and other pituitary hormones. In this connection it may be noted that an apparent association between "thyroid failure" and hepatic dysfunction in man was reported by Lawrence and Rowe.[8] It was stated that the incidence of liver disorder was far more frequent with thyroid disease than with any other endocrinopathy.

The observations cited above thus provide some evidence that through three of its hormones the anterior pituitary may affect liver size—increasing it through prolactin and corticotrophin and decreasing it through thyrotrophin and thyroid action. Moreover, the development and functioning of the sex glands are under pituitary control (gonadotrophin), and sex difference in liver size seems (see below, young and adult Carneaux) to increase with development. It is possible therefore that genetic and endocrine control of both sex and racial difference in liver size is exercised directly or indirectly through the anterior pituitary gland.

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[3] Schooley, J. P., and O. Riddle, Amer. Jour. Anat., 1938, vol. 62, p. 313.

[4] Riddle, O., and R. W. Bates, Proc. Assoc. Res. in Nerv. and Mental Dis., 1936, vol. 17, p. 287; Bates, R. W., O. Riddle, E. L. Lahr, and J. P. Schooley, Amer. Jour. Physiol., 1937, vol. 119, p. 603.

[5] Schooley, J. P., and O. Riddle, Amer. Jour. Anat., 1941, vol. 69, p. 123.

[6] Miller, R. A., and O. Riddle, Endocrinology, 1943, vol. 32, p. 463.

[7] Lee, M. O., and W. Freeman, Endocrinology, 1940, vol. 26, p. 493.

[8] Lawrence, C. H., and A. W. Rowe, Endocrinology, 1928, vol. 12, p. 377; Rowe, A. W., Endocrinology, 1933, vol. 17, p. 1.

Data from Dove Races and Hybrids

Only liver weights from apparently healthy birds are of primary importance in this study, but it seems useful at the outset to provide a summary in which liver weights from dead and diseased birds are included; and also to consider reasons for not regarding some very large livers as valid evidence of disease. Figure 115 shows the distribution of all liver weights obtained from ring dove races for each of the years 1922 to 1944, inclusive; figure 116 gives similar data for ring dove hybrids for the years 1925 to 1944. It will be observed that during most years some liver weights of 16+ gm. (10 per cent or more of the body weight) were observed; these most extreme weights were, of course, obtained in dead or diseased birds, and a part of the excess weight of livers from dead birds is associated with the fact that such birds were not exsanguinated. In 1937 paratyphoid became epidemic in this colony of doves, and thereafter this disease was never completely eliminated. The great length of most of the upper deciles indicates that few birds with extremely heavy livers were obtained. Again, the median values

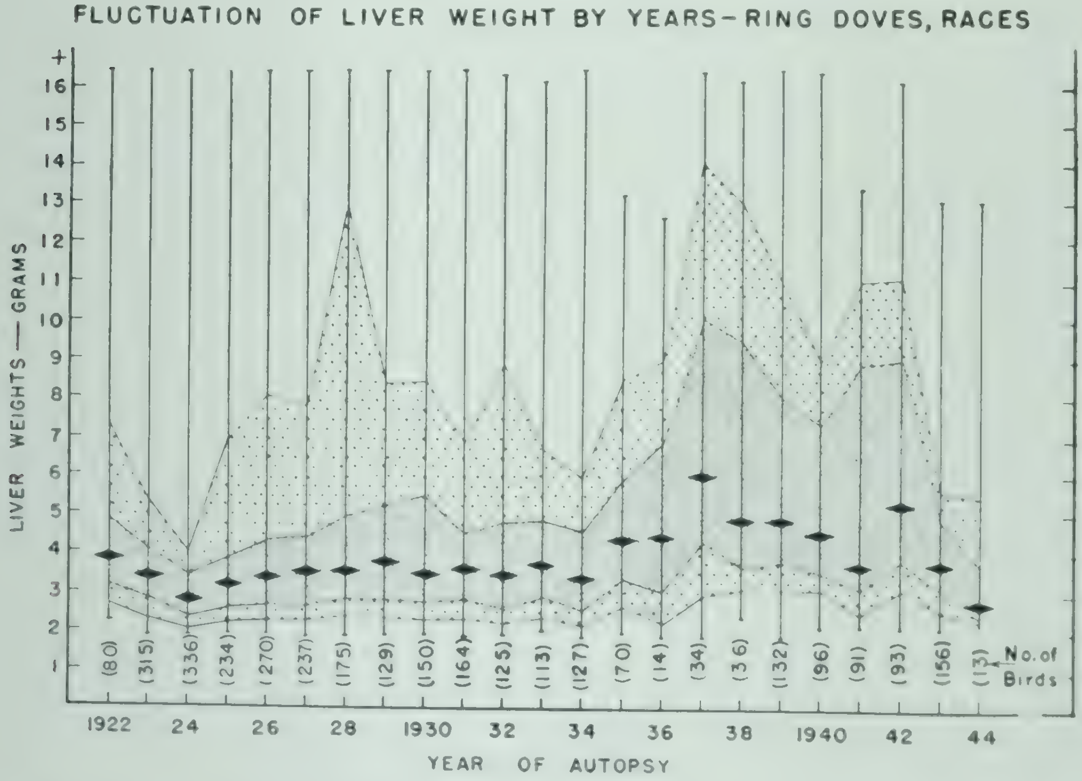


Fig. 115. Showing liver weights obtained from all mature doves (pure races)—healthy, diseased, and dead—for individual years, 1922 to 1944. Medians are indicated in black Heavy stippling marks off upper and lower quartiles. Lines extending beyond lightly stippled areas indicate deciles.

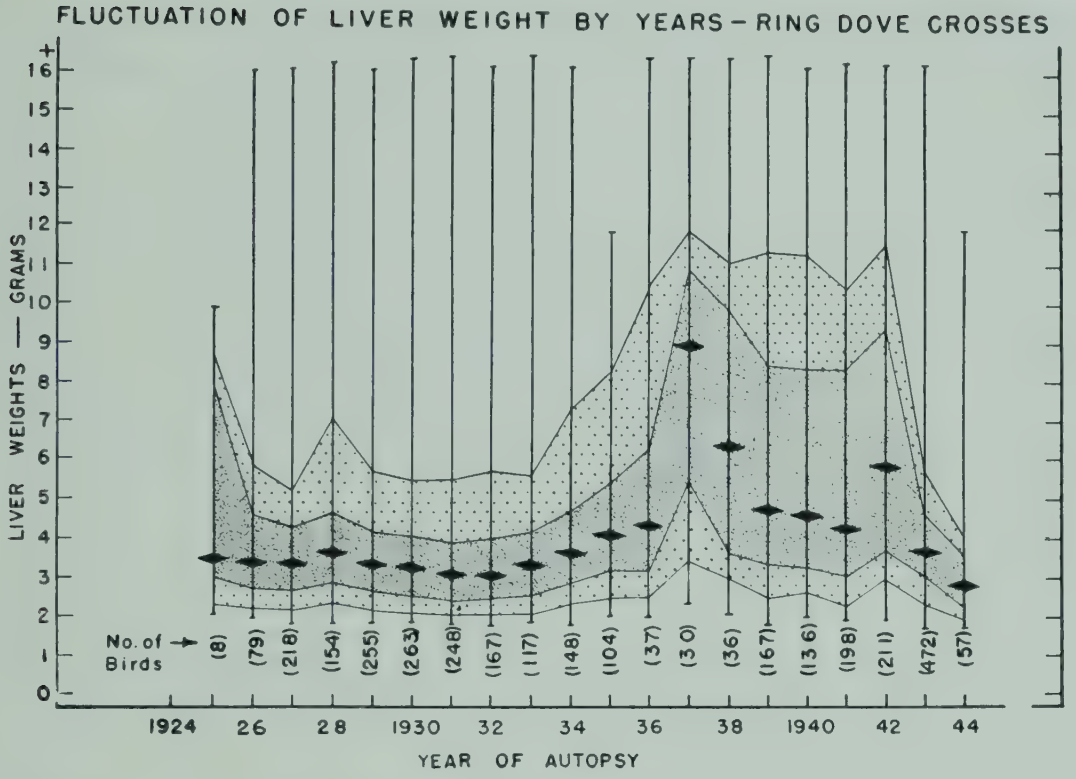


Fig. 116. Showing liver weights obtained from all mature dove hybrids—healthy, diseased, and dead—for individual years, 1925 to 1944. See figure 115 for key to graph. Note the similar trend.

(for races and hybrids alike) for the years 1923 to 1934 are relatively constant despite the inclusion of weights from all dead and diseased birds.

It should now be noted that in the detailed summarization of data which will next be presented, the presence of a very heavy liver, when accompanied by no other indication of disease, did not prevent classification of the bird as "healthy." Though it is fairly certain that this classification was often an error, three relevant facts are to be noted. First, the median values for the birds listed as "healthy" were very little affected by the inclusion of these relatively rare cases of large livers. Second, an occasional female dove with a liver weight of 8 to 13 gm. was found to be in normal, active egg production at the moment she was sacrificed for measurement; and active egg production is nonnegligible evidence of health in doves and pigeons. Third, a threefold *temporary* enlargement of dove livers was produced by means of daily injections of whole anterior pituitary extract; when such livers were examined several weeks after cessation of the injections (unpublished data), no clear evidence (size and histology) of liver injury was obtained. Liver weight in pigeons was classified and analyzed in the same manner as in doves.

A general survey of median liver weight in relation to body weight in apparently healthy birds (including those with ascariasis) of 18 dove races, with separate values for the two sexes, is provided in figure 117. In these races liver weight

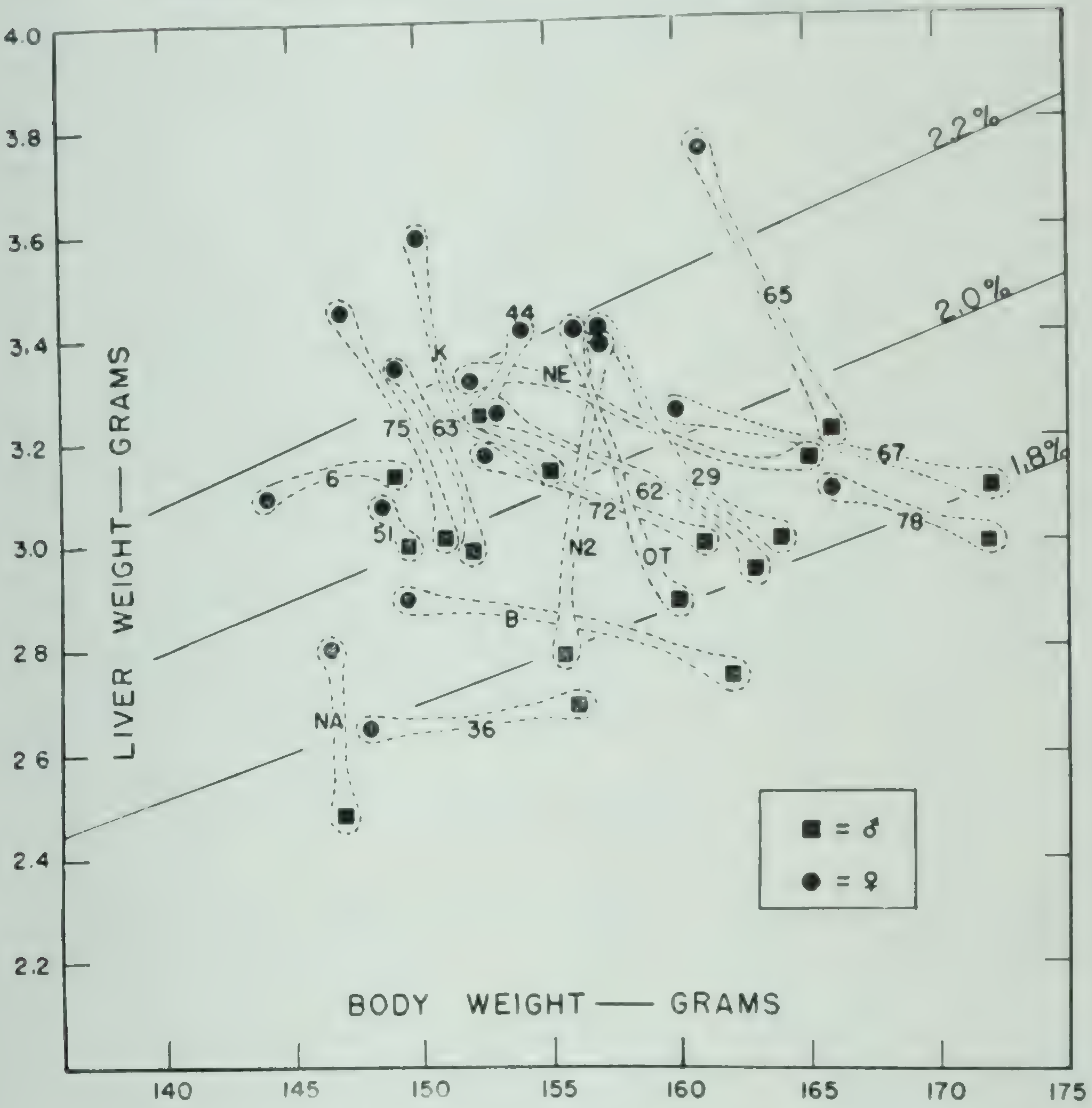


FIG. 117. Graphical survey of median liver weights and body weights in the males and females of 18 dove races. Data from dead and diseased birds are excluded.

was relatively greater in females in all cases, and absolutely greater in all except 2 cases. Within a race (and sex) no close correlation between liver weight and body weight was found. This graph makes it evident that relatively low liver weight characterized races *36*, *NA*, *B*, and *78*. Relatively highest liver weight was found in races *6*, *44*, *K*, and *75*. It is thus clear that races of pure *Streptopelia risoria*, and also races with admixture of another species, are represented at both extremes of liver weight.

Percentile analyses are given for 18 dove races in figures 118 to 123. Coefficients of dispersion for the two groups, healthy and with ascariasis, vary from 0.10 to 0.20. In these analyses data for three health groups are computed separately for the two sexes, and liver weight is also computed in terms of percentage of body weight. Utilizing data provided in these summaries, but omitting pairs for which fewer than 10 birds supplied data for one member, the following average sex

FIG. 118

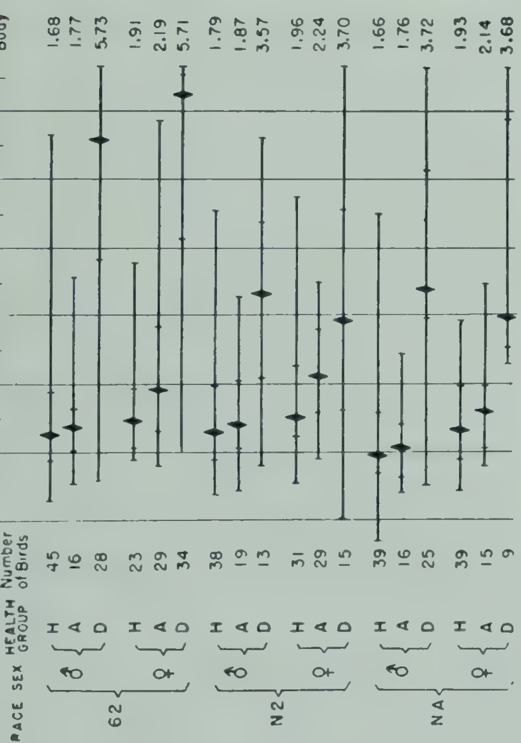


FIG. 119

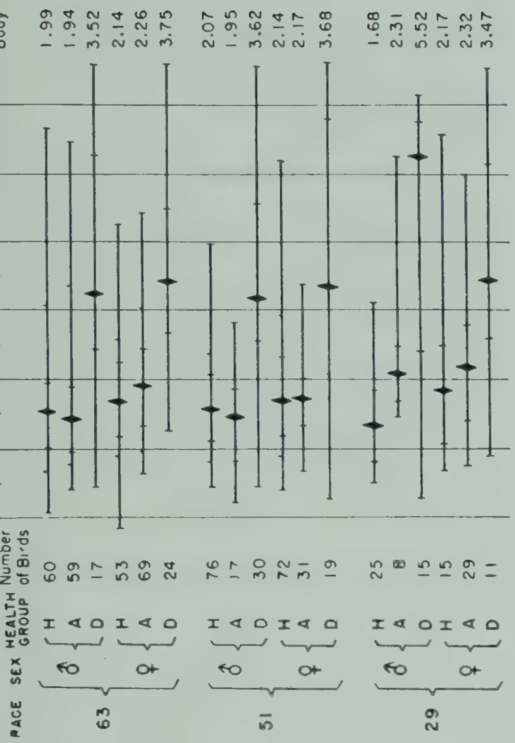


FIG. 120

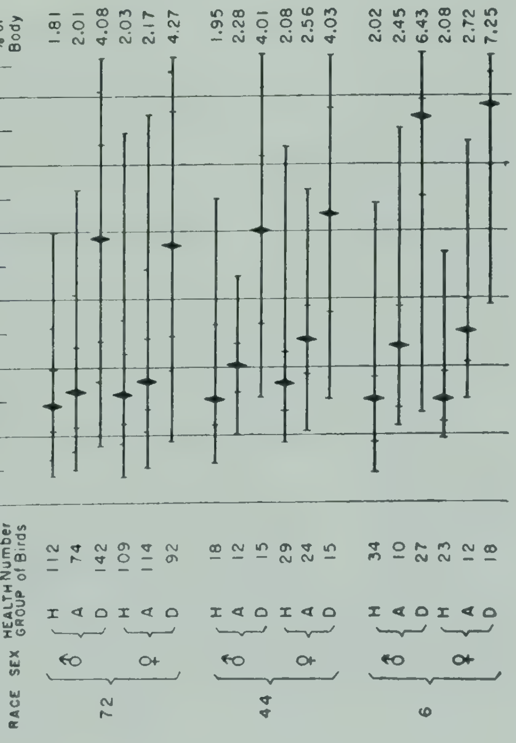


FIG. 121

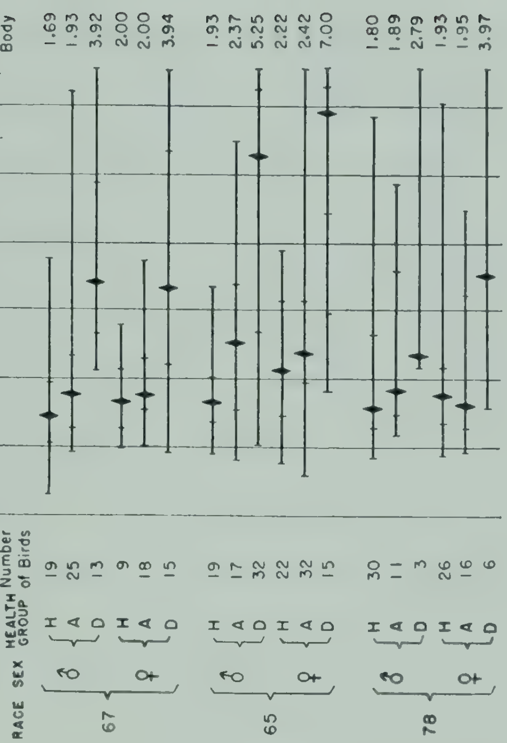


FIG. 122

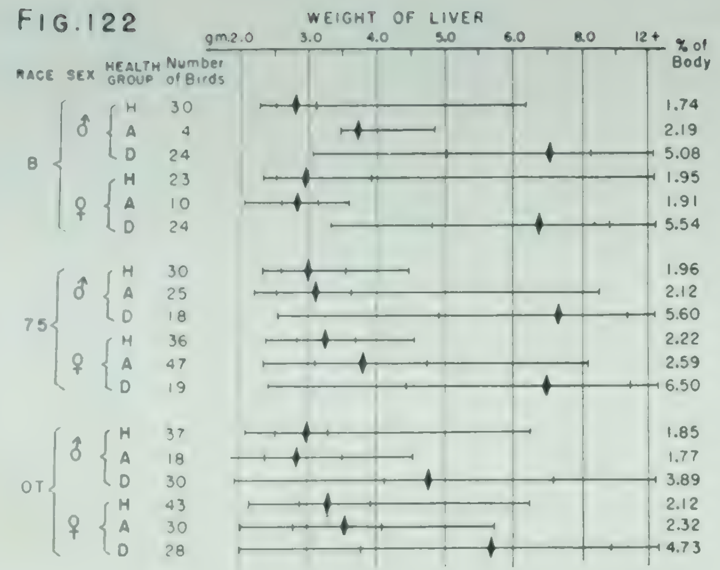


FIG. 123

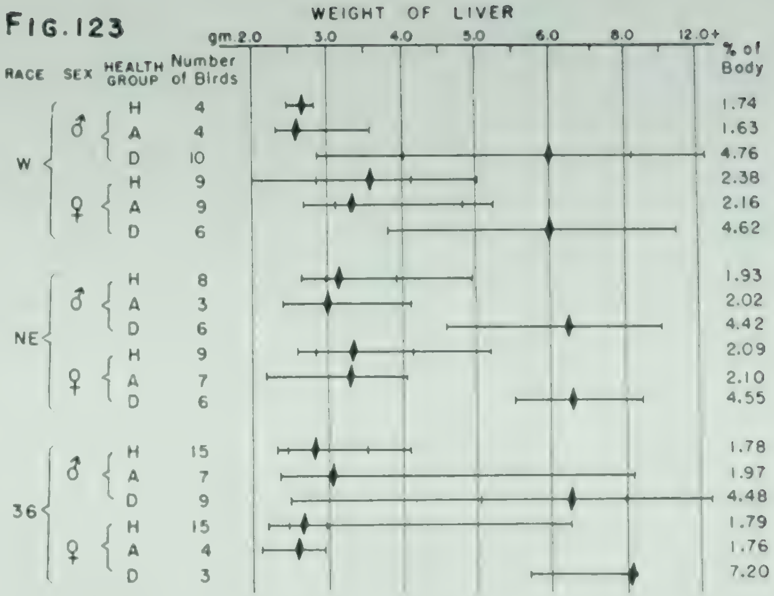


FIG. 124

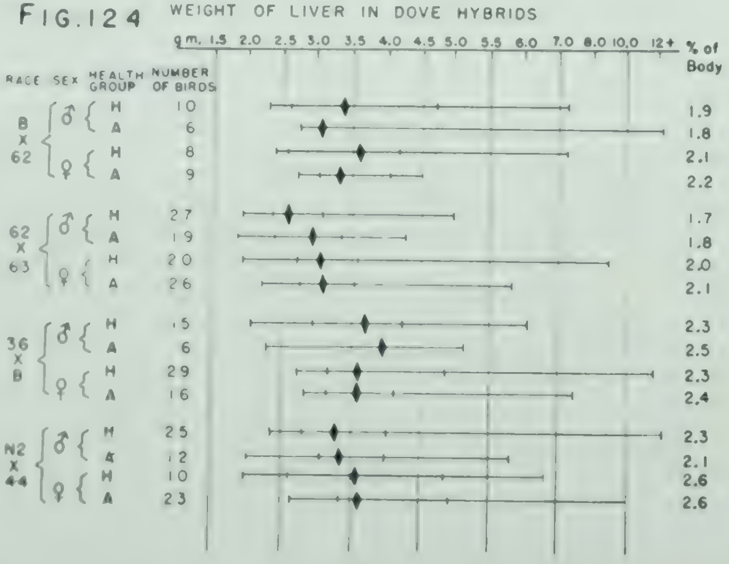


FIG. 125

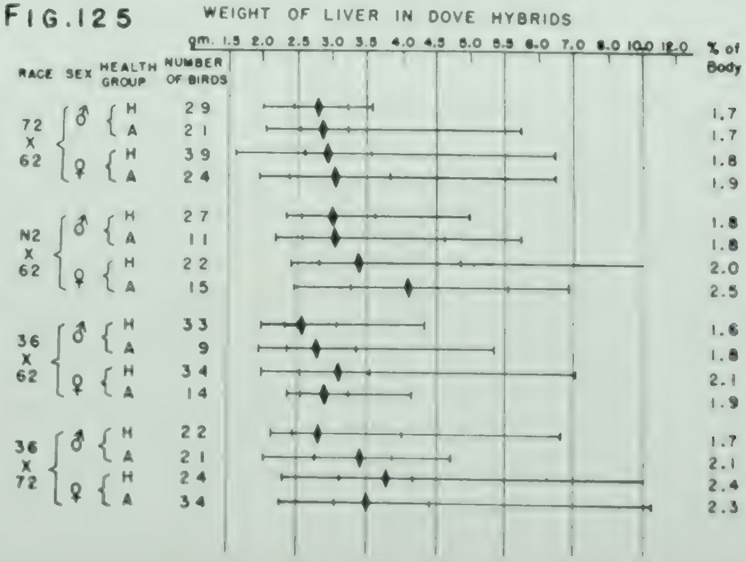
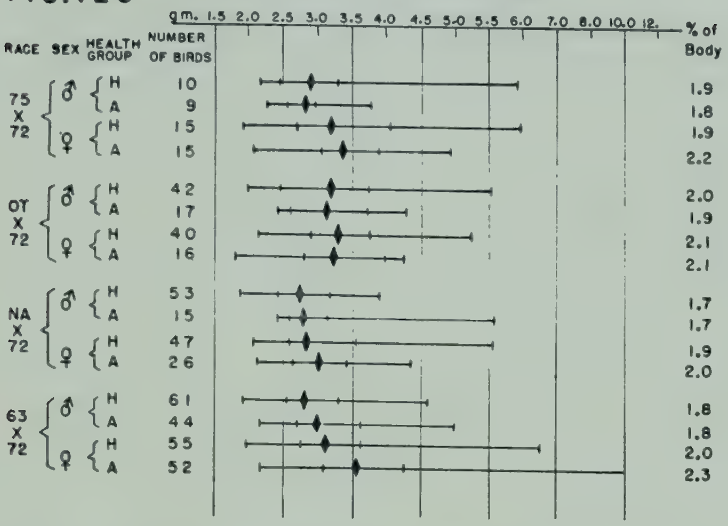


FIG. 126 WEIGHT OF LIVER IN DOVE HYBRIDS



differences were obtained for liver weight expressed as percentage of body weight: Healthy males, 1.85; females, 2.04. *Ascaridia*-infested males, 2.01; females, 2.28. Dead or diseased males, 4.64; females, 4.89. In all the 15 comparisons between "healthy" males and females the relative weight of the liver is greater in the females; on the average this value is 10 per cent greater in females, and for birds with ascariasis this value is 14 per cent greater in females. It is very interesting to observe that the presence of roundworms in the *intestine* is quite generally associated with increased relative weight of the *liver*. Data obtained in the manner just noted provide 23 comparisons between paired measurements within dove races which are entirely comparable except for the presence of ascariasis in one member of the pair. In 21 of the 23 comparisons, relative liver weight was greater in the worm-infested group. This relation is also found (14 of 16 tests) in pure races of pigeons, and perhaps in pigeon hybrids (3 of 4 tests), though it is not observed in less extensive tests on male dove hybrids.

In a consideration of the significance of observed differences in liver weight among dove races, it is only relative liver weight (percentage of body weight) that is usable. The tabulated data, however, provide four usable (dead and diseased birds excluded) percentage values for each race. For race *6* these values are 2.02, 2.45, 2.08, and 2.72; for race *NA* the corresponding values are 1.66, 1.76, 1.93, and 2.14. Thus relative liver weight in race *6* is apparently 24 per cent (mean of 4 measurements) in excess of that in race *NA;* this unquestionably represents a significant difference. Data for additional races may be compared. For race *44* the four values are 1.95, 2.28, 2.08, and 2.56; and for race *B*, 1.74, 2.19, 1.95, and 1.91. In this case the values obtained for race *44* are 14 per cent in excess of those for race *B*. These values, and the similar indications obtained in all of four tests (repeatability), indicate a probably significant difference between the two races. Again, the body weights of races *44* and *36* were practically identical; but liver weight in race *44* exceeded that in race *36* by 25 per cent.

Percentile analyses for 12 types of hybrid doves are given in figures 124 to 126.

Computations similar to those given above (dead and diseased birds omitted) provide the following averages: Healthy males, 1.86; females, 2.10. Males with ascariasis, 1.86; females, 2.22. Data from these two types indicate that liver weight, relative to body weight, is nearly 12 per cent greater in females. The particular hybrid type in which liver weight is relatively lowest is *72* × *62*, followed closely by *N.1* × *72*. Highest relative liver weight is found in hybrids of races *N2* and *44*; and these two races are shown elsewhere to be characterized by extreme length of intestines. This association, together with the fact that injected prolactin lengthens the intestine and increases the weight of the liver, provides an item of evidence that the observed genetic influence is at least partly mediated through the anterior pituitary gland, and, more specifically, through prolactin.

Data from Pigeon Races and Hybrids

A survey of data obtained for 11 races of pigeons is provided in figure 127. In most instances, as was noted earlier in doves, the median liver weight of females exceeds that of males. Liver weight in relation to body weight is relatively low in races *267*, *299*, Magpies (*M*), and Runts (*R*); this value is relatively high in Carneaux (*C*). The measurement was made also on 169 young (2.0–4.0 months) Carneaux. The latter data are not, however, directly comparable with any other data on the chart, since at still earlier ages the livers of pigeons are known to constitute a considerably higher percentage of the body weight than at more advanced ages. The point of real interest in these measurements is that the sex difference in liver weight is less pronounced in young than in adult Carneaux.

Percentile analyses for 10 pigeon races are given in figures 128 to 131. Three health groups for both males and females are analyzed, and liver weight is also given in terms of percentage of body weight. Utilizing data provided in these summaries, but (as was earlier done with doves) omitting pairs for which fewer than 10 birds supplied data for one member, the following differences were obtained for liver weight expressed as percentage of body weight: Healthy males, 1.73; females, 1.87. Males with ascariasis, 1.91; females, 2.08. Dead or diseased males, 2.95; females, 2.95. From pigeon hybrids similar data were obtained: Healthy males, 1.69; females, 1.93. Males with ascariasis, 1.91; females, 2.17. Dead or diseased males, 3.40; females, 3.37. Coefficients of dispersion for the two groups, healthy and with ascariasis, vary between 0.10 and 0.20; this is exceeded in the case of White Kings and Carneaux. These data agree with those obtained from doves in showing relatively heavier livers in females, and an association of roundworms in the intestine with a moderate increase in weight of livers of both sexes.

With due regard to great differences in body weight among pigeon races, the four usable measurements of liver weight may be used to test the significance of differences observed in certain races. Races *267* and *S.1·E* were of similar body weight. Measurements for liver weight in terms of percentage of body weight in race *267* are 1.52, 1.69, 1.50, and 1.68; and in race *S.1 E* (normal only), 1.69, 1.78, 1.90, and 2.02. The means of these values indicate that the livers of the

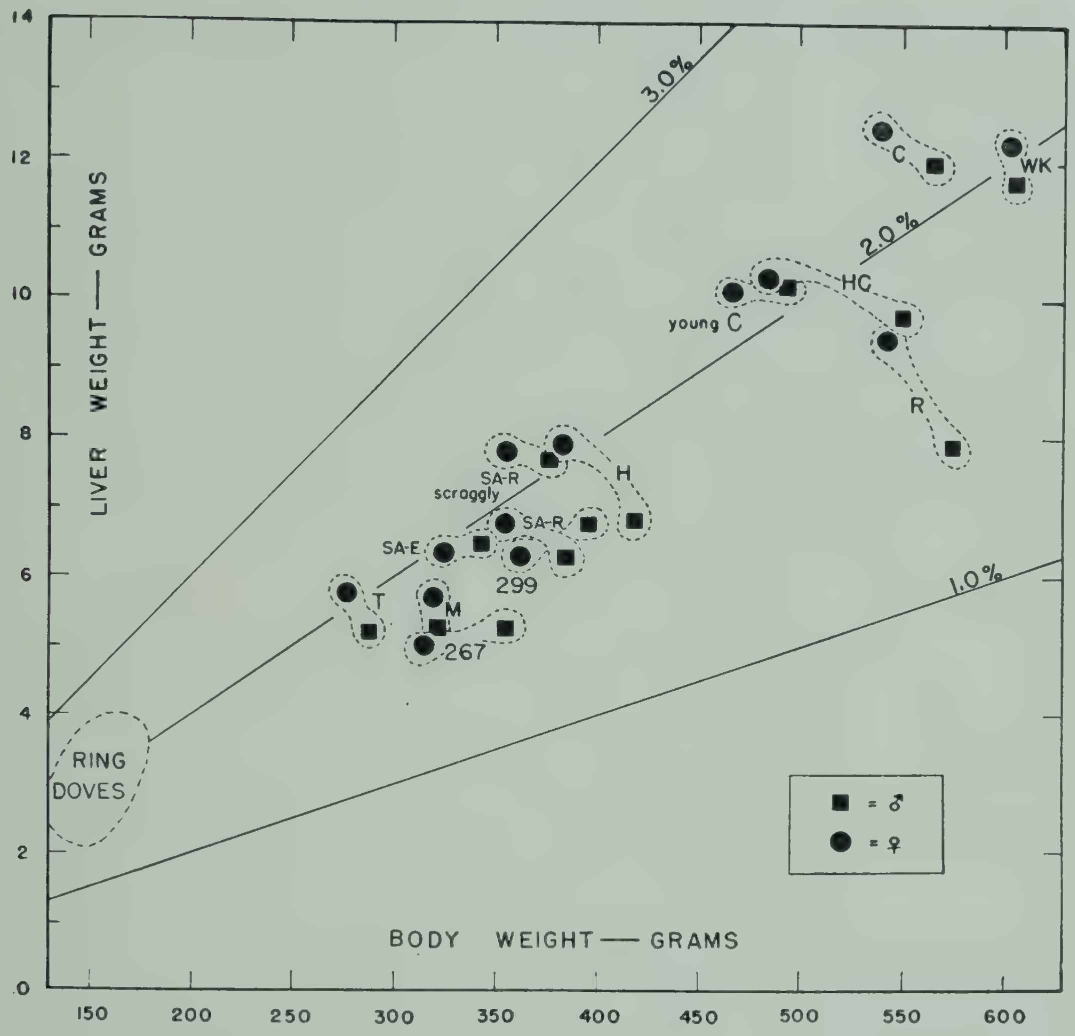


Fig. 127. Graphical survey of median liver weights and body weights in the males and females of 12 pigeon races. Dead and diseased birds excluded. Special data for young Carneaux (91 males, 78 females) show less sex difference in liver weight than is present in adults. In scraggly individuals of race *SA-R* median liver weight is significantly greater than in normal individuals of that race.

latter race exceeded those of the former by nearly 16 per cent. Again, Runts and Carneaux were approximately equal in body weight. Their liver weights, in terms of percentage of body weight, follow: Runts, 1.36, 1.47, 1.74, and 1.63; Carneaux, 2.04, 2.45, 2.07, and 2.40. The livers of Carneaux are thus found to exceed those of Runts by 44 per cent.

Liver weight within the three types (normal, scraggly, ataxic) which compose race *SA-E* requires mention. These types were approximately equal in body weight. Their liver weights, expressed as percentage of body weight and as a single mean value, follow: normals, 1.80; scraggly, 1.95; ataxic, 1.78. Percentile analyses are not shown for race *SA-R*, but its normal and scraggly types are separately represented on the survey chart (fig. 127). The scraggly type again had significantly (12 per cent) larger livers than the normal type. In part II of this

FIG. 128

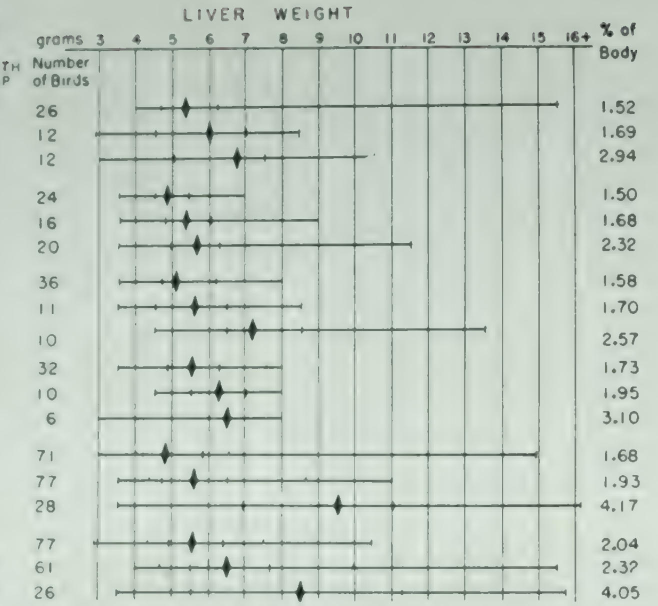


FIG. 129

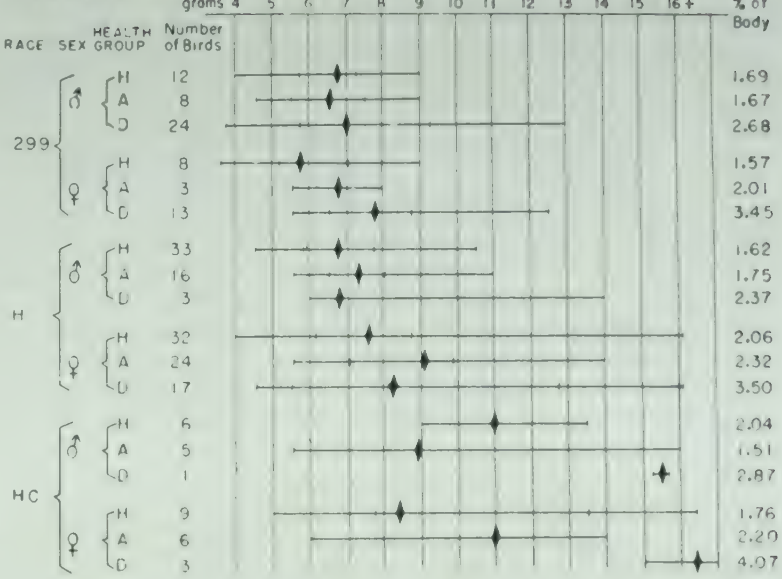


FIG. 130 LIVER WEIGHT IN RUNT, KING AND CARNEAU PIGEONS

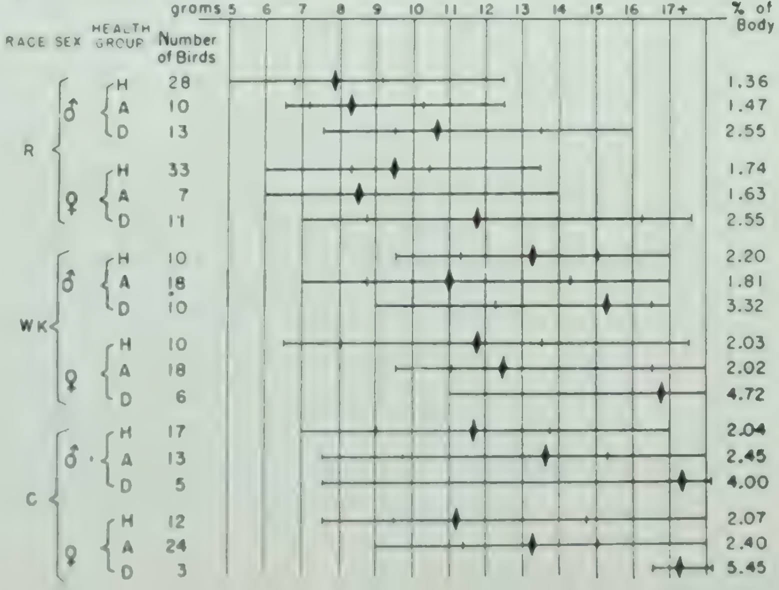


FIG. 131

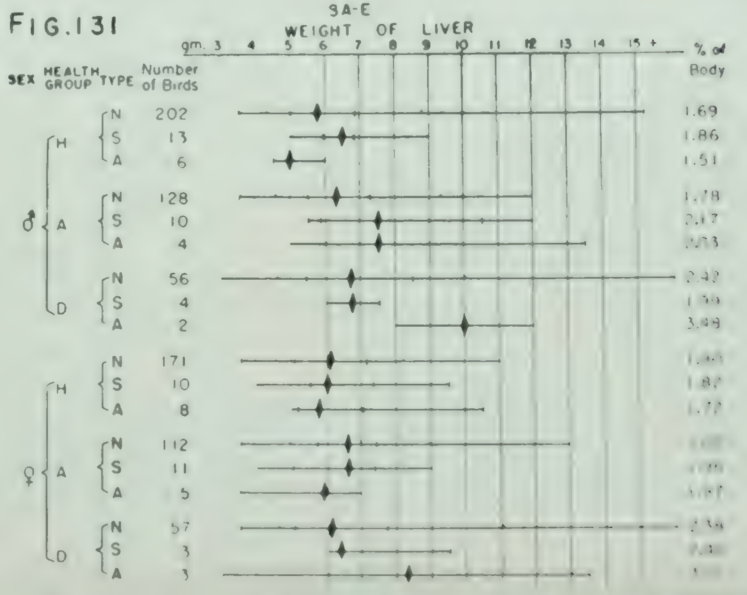


FIG.132

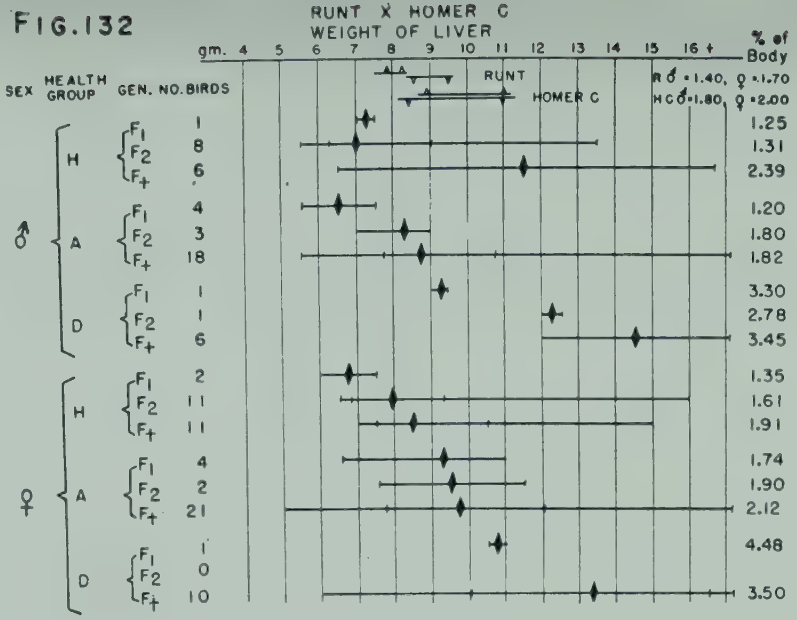


FIG.133

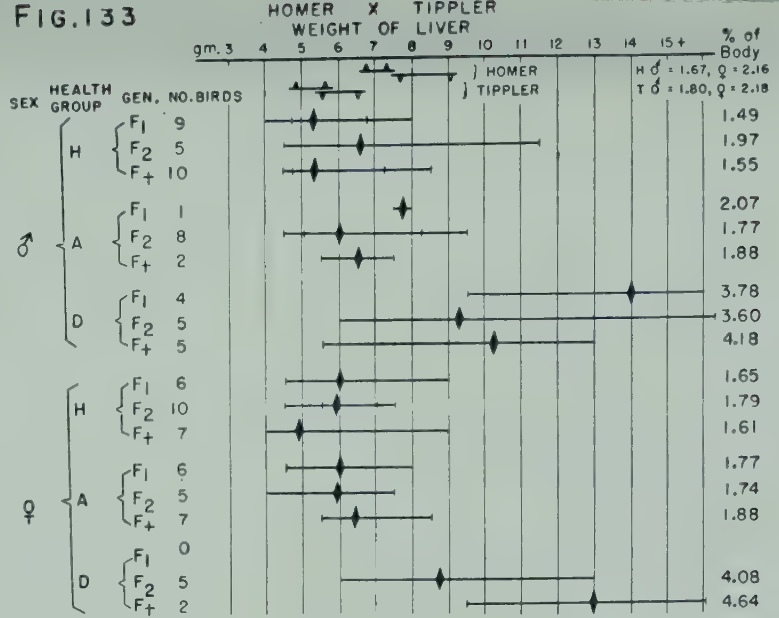


FIG.134

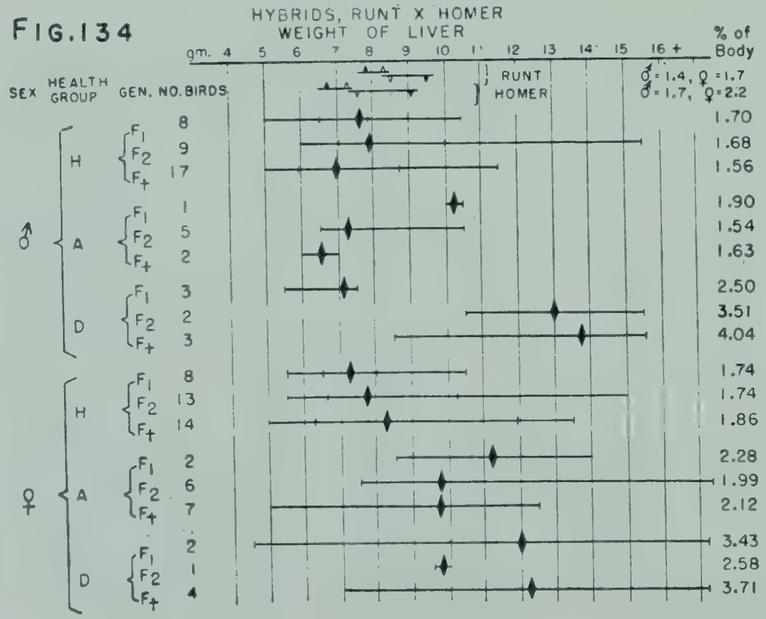


FIG.135

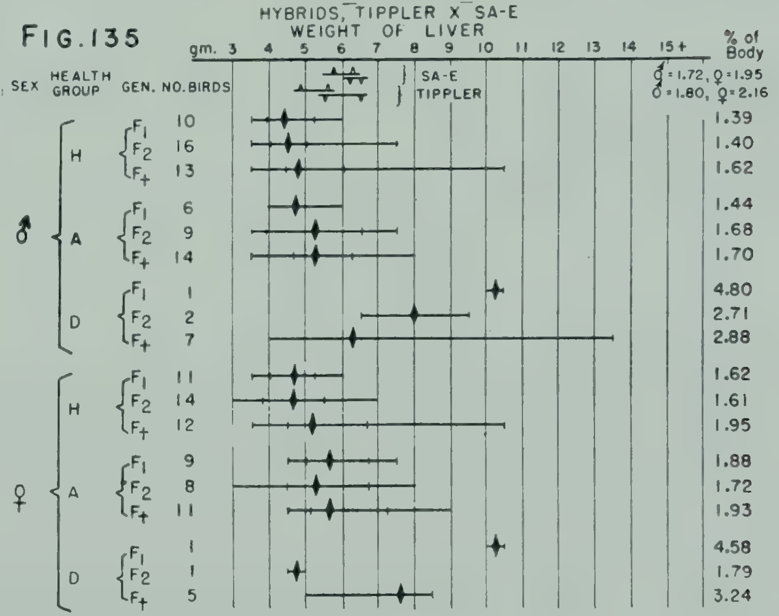


FIG.136

HYBRIDS, RUNT X SA-E
WEIGHT OF LIVER

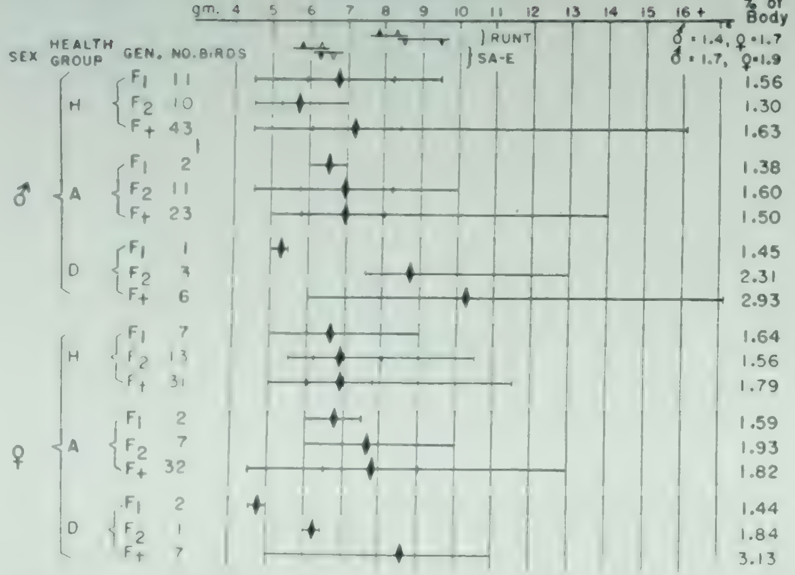


FIG.137

RUNT X MAGPIE
WEIGHT OF LIVER

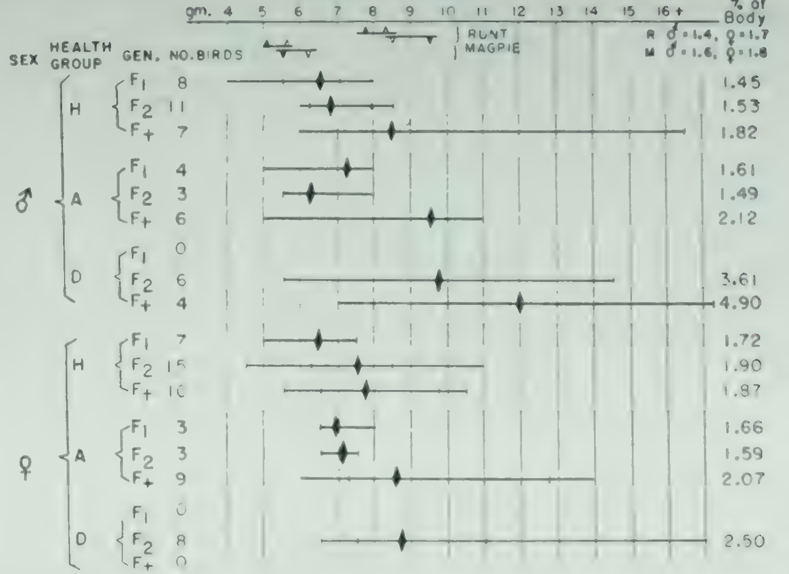


FIG.138

HYBRIDS, RUNT X 299
WEIGHT OF LIVER

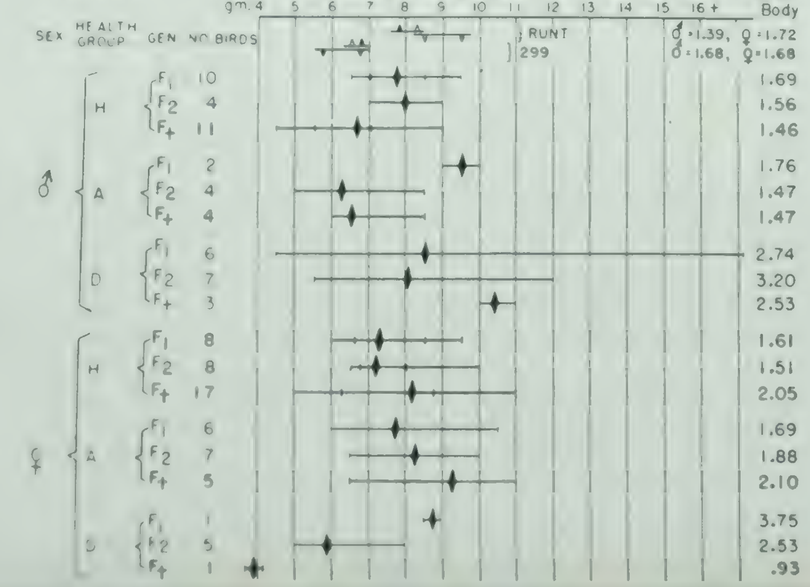


FIG.139

TIPPLER X 267
WEIGHT OF LIVER

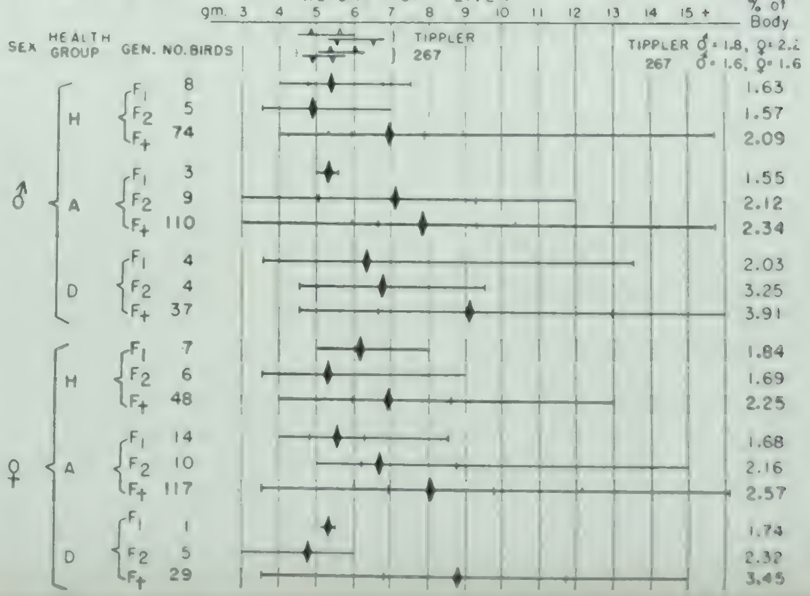
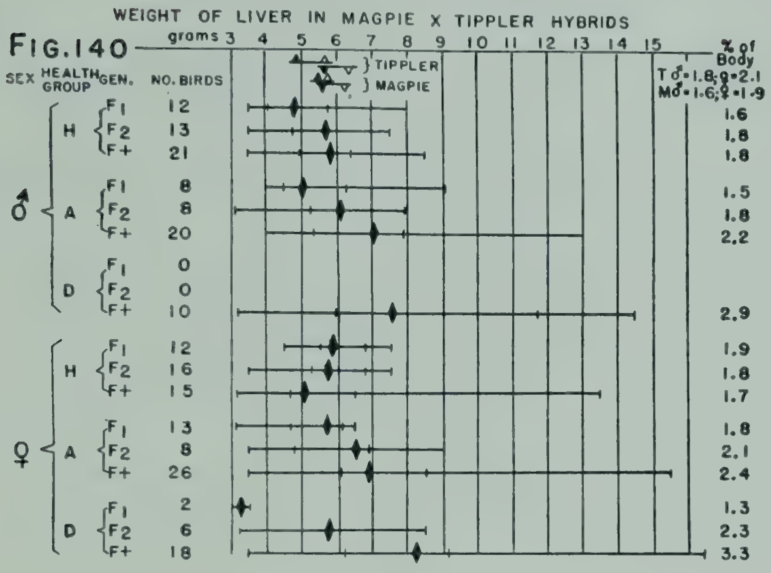


FIG. 140



WEIGHT OF LIVER IN MAGPIE X TIPPLER HYBRIDS

volume the scraggly type is found to show, in association with its defective plumage, an extremely high rate of basal metabolism. That high expenditure of energy implies increased food consumption, and in this particular case increased liver weight is probably attributable to the ingestion of unusual quantities of food. Ataxic birds appear to show liver weights nearly identical with those of normals, but the number of ataxics studied is rather small for a satisfactory measurement.

Measurements of liver weight in pigeon hybrids are analyzed and presented in figures 132 to 140. The data for F_1, F_2, and F_+ generations are given separately. Also, at the top of each table graphic devices or lines are used to indicate median values obtained for each sex (males above, females below) of each parent race; a solid half-diamond pointer indicates the median obtained from healthy birds, and an open half-diamond marks the median obtained from birds with ascariasis. With the aid of these devices it is easy to determine the relation which the several values for hybrids bear to the median values for the parental races.

In nearly all cases in which fair numbers are available, F_1 liver weights are intermediate to those of the parental races. The same is true for F_2. Only in Tippler × *SA-E* hybrids do liver weights of F_1 and F_2 tend to be actually less than those of either parental race. In several kinds of hybrids (*R* × *HC*, *T* × *SA-E*, *R* × *SA-E*, *M* × *T*, *R* × *M*, and *T* × *267*) there is a tendency for the liver weights of F_+ to exceed those of either F_1 or F_2. The meaning of this trend is not clear. Perhaps heterosis in F_1 produces a more efficient liver and the efficient liver is small; thereafter, regression to large size in F_+ would naturally follow. Possibly unrecognized disease resulting in liver enlargement was more prevalent in later than in earlier years of the test; this would tend to produce the observed result, since it is probable that a greater proportion of F_+ than of earlier generations were measured during the later years of the test.

Summary

In concurrent studies it was learned that endocrine factors are significant in the regulation of liver weight in doves and pigeons. When used experimentally, the pituitary hormone prolactin tended to increase liver weight, as did adrenal cortical hormone; thyroxin tended to decrease it. Seasonal and other conditions also provided evidence that prolactin increases and thyroid activity decreases liver size in these animals.

Liver size is very commonly affected, usually increased, by disease. Though most diseased livers were excluded from those classed as healthy in this study, some diseased livers were doubtless included. Because of the statistical method used (percentile analysis), these inclusions probably do not seriously affect the validity of the present measurements.

In both doves and pigeons the livers of females are relatively (usually also absolutely in doves) heavier than those of males. In data from doves this excess averaged 10 to 14 per cent; in pigeons it was somewhat smaller and more variable.

The presence of roundworms (ascariasis) in the intestines of doves and pigeons is associated with an increase in weight of the liver. Otherwise healthy birds are therefore separated for purposes of measurement into groups which were, and were not, parasitized by these roundworms.

Relatively low liver weight characterized ring dove races *36*, *NA*, *B*, and *78*. Relatively high liver weight characterized races *6*, *44*, *K*, and *75*. Significant differences were found between some of these races.

Among the long-established breeds of pigeons, liver weight was found to be relatively low in Runts and high in Carneaux. The difference equals 44 per cent of the weight of the Runt liver. Among our own pigeon races, relatively small livers characterized races *267* and *299*.

Normal and scraggly individuals of race *S.A-R* show a difference of 12 per cent in median liver weight. In *S.A-E* the scraggly birds showed an excess of about 8 per cent. This excess liver weight in scragglies is probably environmentally induced, in association with their extremely high basal metabolic rate and (probable) high food intake.

Liver weight in F_1 and F_2 hybrids from pigeon races tended to be intermediate to that in the parental races.

The control of both racial and sex (genetic) differences in liver weight observed in this study is probably accomplished by genetic factors which act through or upon the anterior pituitary gland.

7

AGE AT SEXUAL MATURITY AS A RACIAL CHARACTER

Introductory Statement

The age at which the first egg is laid is a definite point, and an easily observed event, in the life of a dove or pigeon. To ascertain this same point in the life of humans and other mammals is by no means a simple matter. Moreover, it seems that in the female bird the age at which the first egg is laid may properly be regarded as the age at which the bird becomes sexually mature. When first steps were taken to establish the series of races of ring doves, it was well known that individual females of the dove colony matured at very different ages, and that fact was utilized by including some early-maturing and some late-maturing individuals among the females selected as parents for the 24 races. Indeed, this difference in age of maturity was regarded as one of the most significant items that we had observed in connection with the reproductive records of these birds. On a priori grounds it was considered probable, first, that this character had a hereditary basis; and, second, that the hereditary control was exercised through one or more endocrine glands. Two quite relevant facts, however, were entirely unknown at that time: First, the season (month) of origin of the bird has an important influence on the age at which sexual maturity is attained. Preliminary statements on that point have been published.[1] Second, Smith and Engle,[2] and Zondek and Aschheim,[3] later showed that a hormone of the anterior pituitary gland controls the growth and maturity of the gonads of mammals. Soon thereafter Riddle and Flemion[4] extended this observation to doves and pigeons.

The three studies last named made it appear probable that if a hereditary control of "age at maturity" exists in doves and pigeons, such control is exercised through the anterior pituitary gland, and indeed through that fraction of the gland (basophilic cells) which secretes gonad-stimulating hormone. It was shown by Riddle and Schooley[5] that up to the age of about 2.5 months the pituitaries of doves and pigeons do not contain detectable amounts of gonad-stimulating hormone; and in another study[6] these observers obtained apparently conclusive evidence that in adult pigeons, as had been shown by others for mammals, the basophilic cells are the source of gonadotrophic hormone. Still other studies have indicated that light rays, which vary with season, are capable of modifying the output of the gonad stimulating hormone in the pituitaries of adult birds and mammals.[7] It has thus become evident, therefore, that the pituitary basophils are a channel through which both hereditary (racial) and environmental (seasonal) factors may influence the age at which an individual bird becomes sexually mature.

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[1] Riddle, O., Amer. Jour. Physiol., 1931, vol. 97, p. 581; Carnegie Inst. Wash. Year Book no. 42, 1943, p. 136.

[2] Smith, P. E., and E. T. Engle, Amer. Jour. Anat., 1927, vol. 40, p. 159.

[3] Zondek, B., and S. Aschheim, Klin. Wochenschr., 1927, vol. 6, p. 248.

[4] Riddle, O., and F. Flemion, Amer. Jour. Physiol., 1928, vol. 87, p. 110.

[5] Riddle, O., and J. P. Schooley, Proc. Soc. Exper. Biol. and Med., 1935, vol. 32, p. 1610.

[6] Schooley, J. P., and O. Riddle, Amer. Jour. Anat., 1938, vol. 62, p. 313.

Information on the inheritance in fowl of early and late maturity, and indeed on the formation of such races by selection, is now available. Dunn[8] observed that maturity was postponed in inbred fowl and hastened in the F_1 obtained from crosses of inbred strains. From one original stock of Rhode Island Red hens Warren[9] selected two strains which differed in mean age of maturity by as much as 40 days. Both sex-linked and autosomal factors seemed to be involved in the determination of this difference. Asmundson[10] obtained similar results in turkeys (*Meleagris gallopavo*), and reached similar conclusions as to the factors concerned in the inheritance of this character. The same author[11] later reported evidence indicating that when artificial light is used to hasten sexual maturity, the threshold of response is lower in turkeys than in fowl.

Certain facts of practical importance concerning the present data should be mentioned here. From the age of slightly less than 2 months to maturity all young females were kept in large pens with groups (20 to 50) of other maturing males and females. The males of these groups always provided adequate stimulus to copulation long before the females were able to produce eggs. When a female dove or pigeon releases an egg from her ovary she also exhibits an interest in a nest (nests were provided for this purpose), and by sitting on a nest she warns that an egg is being formed. In such birds the ovulated egg can be palpated within the oviduct during a period of 33 hours before the egg is due to be laid. The pens containing maturing birds were inspected twice daily and, with rare exceptions, the ovulating females were recognized and isolated. Soon after these females were placed in a separate cage a mate was provided, and the entire record of reproductive performance of the pair was obtained through daily inspections of their nest.

Dove Races and Their Hybrids

The age, in months, at which sexual maturity was attained in the females used to start the 24 dove races, together with the date of the egg from which each of these females was derived, is given in table 11. It will be observed that one of these females (race *29*) reached sexual maturity at the age of only 4.7 months, whereas another female (race 72) attained maturity at 10.9 months. All other females attained maturity at intermediate ages.

Data for all (1181) dove hybrids are presented in figure 141 in a form that

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[7] For a review of the studies of Rowan, Bissonnette, Baker, Benoit, and others, see Marshall, F. H. A., Biol. Reviews, 1942, vol. 17, p. 68.

[8] Dunn, L. C., Ztschr. f. indukt. Abstam.- u. Vererbungsl., suppt. vol. 1, 1928, p. 39.

[9] Warren, D. C., Genetics, 1934, vol. 19, p. 600.

[10] Asmundson, V. S., Amer. Naturalist, 1939, vol. 73, p. 365.

[11] Asmundson, V. S., Poultry Sci., 1941, vol. 20, p. 51.

TABLE 11

DATA FOR SEASON OF ORIGIN AND AGE (IN MONTHS) AT SEXUAL MATURITY OF THE FEMALES SELECTED AS STARTING POINT OF TWENTY-FOUR DOVE RACES

Race	Date of egg of origin	Age at maturity	Race	Date of egg of origin	Age at maturity	Race	Date of egg of origin	Age at maturity
29.......	6/1	4.7	36.......	3/15	6.2	NA......	7/9	9.0
N2......	10/8	4.9	1........	6/12	6.4	206......	4/8	9.3
78.......	3/14	5.2	69.......	4/27	6.7	62.......	5/28	9.8
63*c*......	1/22	5.3	51.......	4/20	7.8	44.......	2/4	9.8
61.......	9/20	5.5	67.......	1/21	7.9	NE......	3/29	10.1
63.......	2/26	(6.0)*	163......	8/8	8.3	11.......	3/19	10.1
O........	10/1	6.0†	65.......	7/24	8.6	75.......	3/12	10.4
OT......	10/1	6.0†	6........	5/24	8.8	72.......	6/27	10.9

*The first egg of this bird (♀A622) was not identified. The value given is the average age of maturity of her 5 daughters by a related male.

†The same female was used to initiate races O and OT.

indicates the variability of age at maturity. The distribution shown there is considered the normal for ring doves as a species. The top deciles are not fully indicated; at every month of the year one or more individuals were found which matured at an age greater than 12 months, and for some of these the age at maturity exceeded 16 months. The earliest observed age of maturity in a dove was 4.0 months. The very wide spread of quartiles in January and February reflects the fact that the data, if otherwise plotted, would show a distinctly bimodal distribution at these periods.

Since the line connecting the monthly medians is quite representative of the trend, it alone is used in the subsequent figures. In figure 142 two contrasting pure races of doves, and two typical races of pigeons, are so plotted as to illustrate the differences shown by the data. Races *72* and *63* represent, approximately, the extremes of age at maturity in the different dove races. It is of interest to note that neither of these races has an infusion of blood from another species.

Only those dove races for which sufficiently large numbers are available require consideration here. It is evident that age at maturity is a highly variable character apart from season of origin, and that the seasonal factor cannot be ignored in any race of ring doves. The usable data from other races than the two hitherto described are presented in figure 143. The curves relate only to those months in which greatest numbers of young doves were hatched; and these particular curves were smoothed by the method of three-point "moving medians." The line labeled *X* on this graph again represents median values obtained from all dove crosses; that line supplies a standard against which early and late maturity may be judged. In addition to race *72*, races *NA*, *51*, *N2*, *65*, and (perhaps) *75* were predominantly late-maturing populations. Races *44* and *78* were early-maturing populations; the curves which describe this fact, however, unlike those

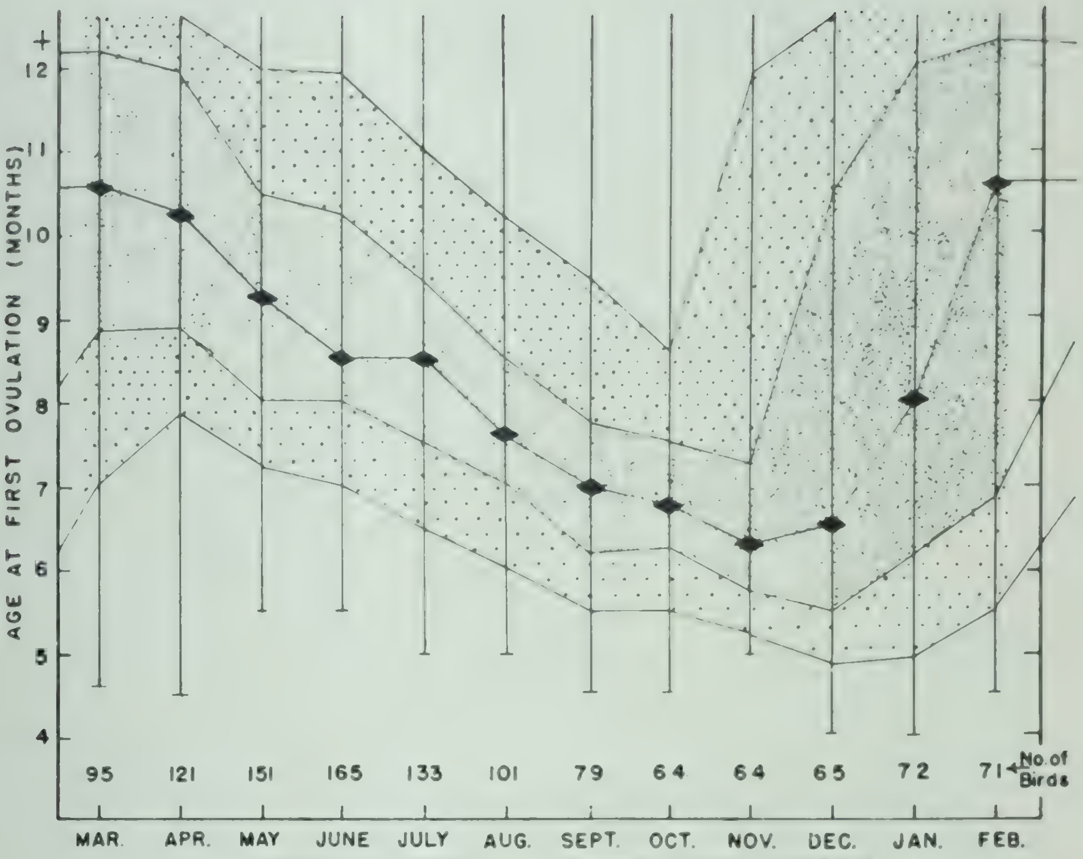


FIG. 141. Seasonal fluctuation of age at first ovulation in dove hybrids. The variability found in data for 1181 females is shown. Lines extending beyond lightly stippled areas indicate deciles.

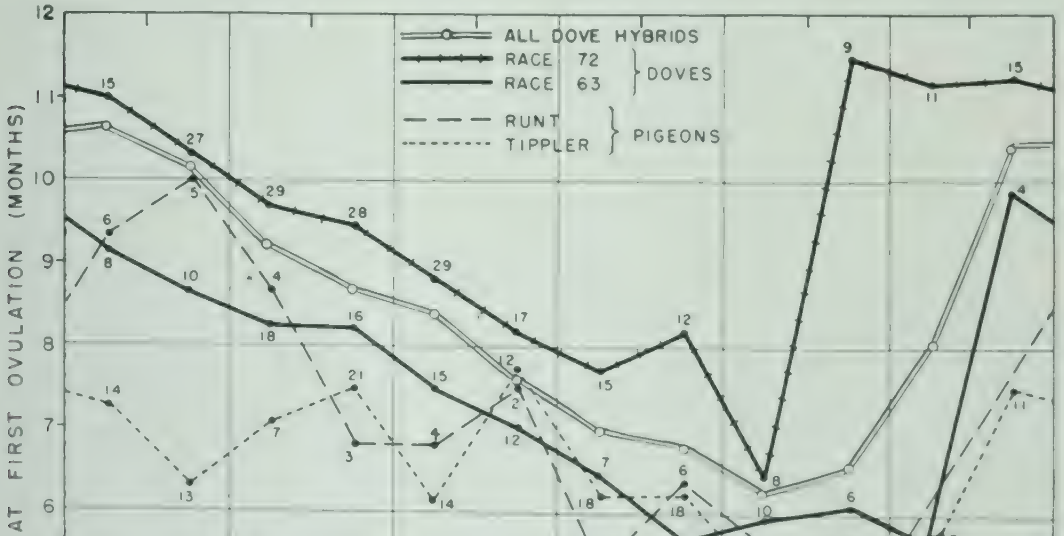


FIG. 142. Seasonal but parallel fluctuation of age at first ovulation in females of various races of ring doves and in 2 representative breeds of pigeons. The points on the curves are median values for the number of birds indicated by the numerals.

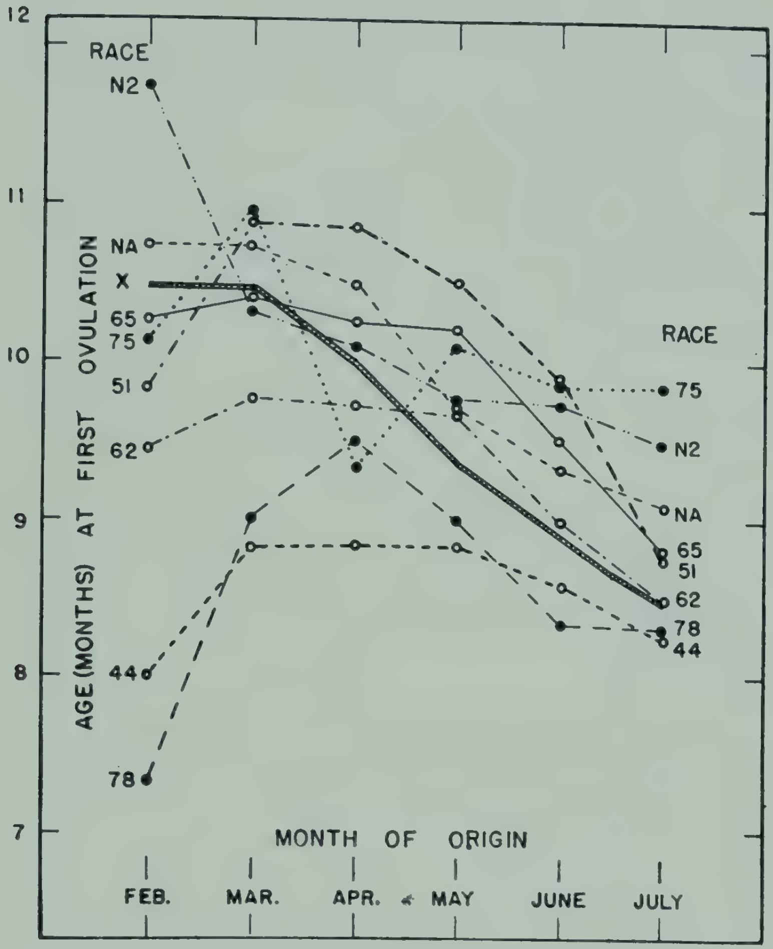


FIG. 143. Seasonal fluctuation of age of first ovulation in females of various races of ring doves. Adequate data were not available for the part of the year (August to March) not represented on the graph. The heavy line (*X*) represents median values obtained from all dove hybrids.

for race *63* and other large groups, do not show the usual pattern of seasonal influence. The available data indicate that birds of races *44* and *78* matured slightly later than those of race *63;* and that races *NA* and *51* matured approximately as late as did race 72.

In the various crosses it was rarely possible to obtain sufficient numbers of F_1 females to warrant a definite conclusion as to their age at maturity. In general, however, they appear to tend toward early maturity. In the cross of *NA* × 72 (both late-maturing), maturity in the F_1 tended to be late except in birds originating during June through November, which tended to mature early; but since this result rests on data from only 14 birds, its significance is questionable. There is therefore little evidence for heterosis in this trait, though earliness of maturity is probably dominant.

The later (F_2 and F_+) generations of 72 × *63* show a trend to intermediacy between the parental races (table 12); exceptions are observed for 4 months when data from very few (3, 3, 3, and 4) birds were available. *NA* × 72 hybrids,

TABLE 12

MEDIAN AGE AT MATURITY OF HYBRIDS (F_1 OMITTED) OF RACES 63 AND 72

Month	Median age (months)	No. of birds	Month	Median age (months)	No. of birds
March	9.0	3	September	7.6	7
April	10.3	12	October	7.3	4
May	8.5	5	November	6.1	6
June	8.6	11	December	5.5	3
July	8.8	3	January	10.8	9
August	8.1	7	February	11.4	4

of which 60 birds are available, are as late as or later than race *72* in only 3 of the 12 months, although the exceptional birds also tended to mature later than did birds of race *63*. It is noteworthy, however, that for the cross of races *44* and *63* (both early-maturing races), the F_2 and F. birds tended to mature less early than the parent races.

PIGEON RACES AND THEIR HYBRIDS

Despite their larger body size, pigeons tend to mature earlier than ring doves. The influence of season on age at maturity also has proved to be less in pigeons than in doves. Some evidence supporting both these conclusions is found in the data of figure 142, in which data for Runts and Tipplers are plotted alongside data for ring dove races and hybrids. In the general analysis of data for pigeon types (figs. 144–154), the seasonal factor has been ignored; medians, quartiles, and deciles are calculated, and information concerning population size is given. Two types of females did not contribute to the data thus analyzed: First, those designated "no record" include females killed or dead while immature. Second, a small group of "barren" females, essentially healthy (otherwise called "old virgins"), were killed at ages greater than 12 months with no record of egg production.

The graphs which present the data on age at maturity include also data on testis weight in the adult males of the same types. Although the latter data will be described in a subsequent chapter, it has seemed advantageous to plot the two kinds of data on the same graph.

Data for age at maturity of 10 pigeon races are shown in figures 144 and 145. The median age at maturity was latest in Homers *C* (*HC*; 9.9 months) and Magpies (*M*; 9.8 months); it was earliest in Homers (*H*; 6.5 months) and Tipplers (*T*; 6.55 months), but only slightly later in Runts (*R*; 6.92 months) and *S.A-E* (6.96 months). Other races (White Kings, Carneaux, *267*, and *299*) matured at intermediate ages. It is thus fairly clear that the procedures used, decades or centuries ago, in the establishment of so-called standard varieties of pigeons resulted in the segregation of genetic factors for age at maturity.

FIG. 144

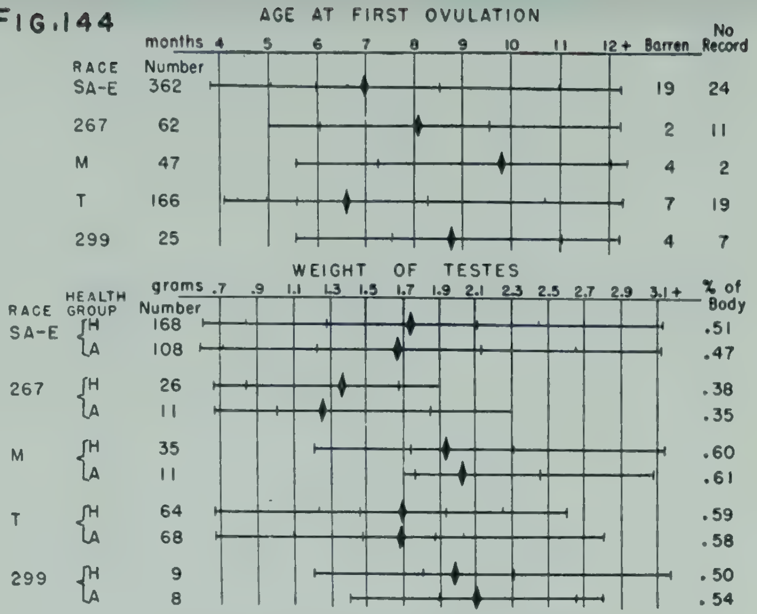
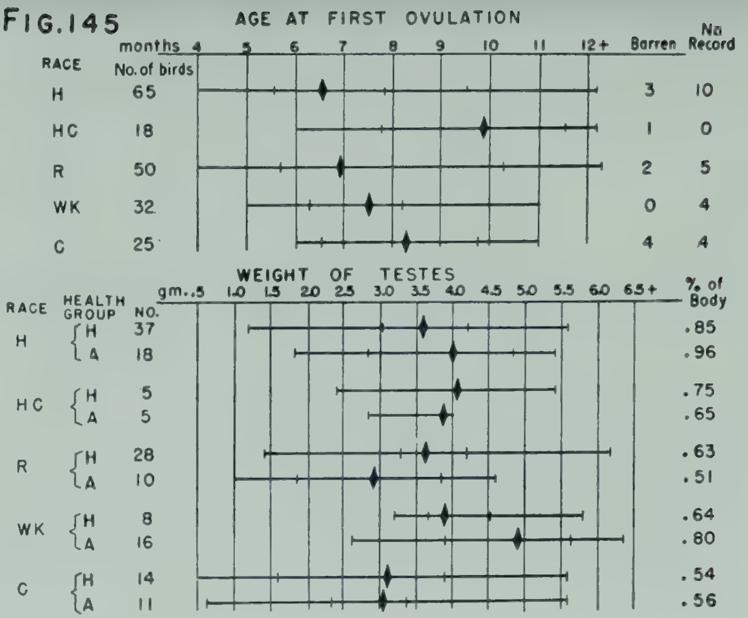
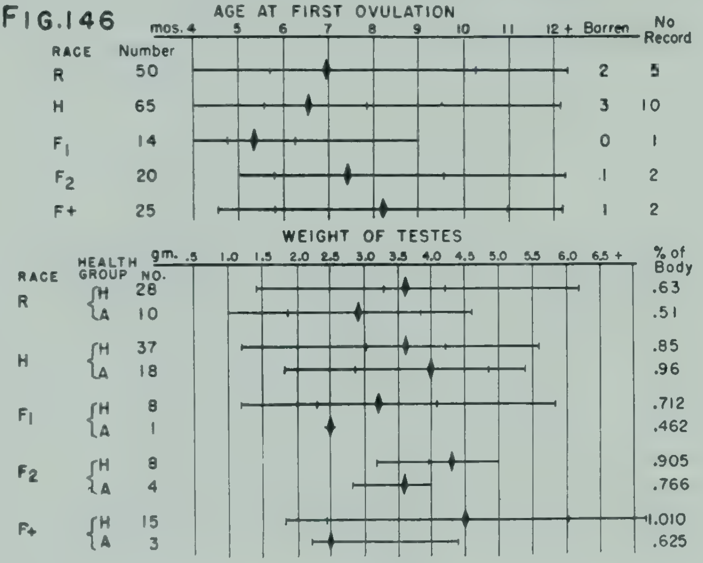


FIG. 145



RUNT AND HOMER RACES AND THEIR HYBRIDS

FIG. 146



FIGS. 144–154. To facilitate a comparison of size of testes with age at ovulation (in each race or type), these two items are brought together. The data relating to weight of testes are discussed in the following chapter.

FIG. 147

RUNT AND SA-E RACES AND THEIR HYBRIDS

AGE AT FIRST OVULATION

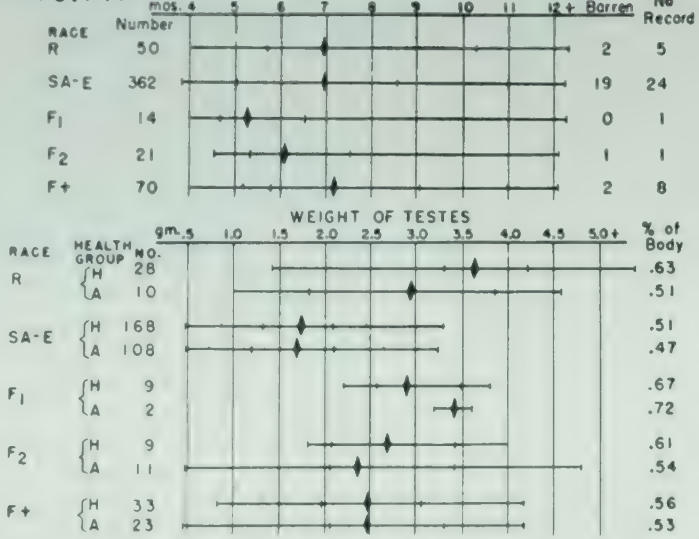


FIG. 148

RUNT AND MAGPIE RACES AND THEIR HYBRIDS

AGE AT FIRST OVULATION

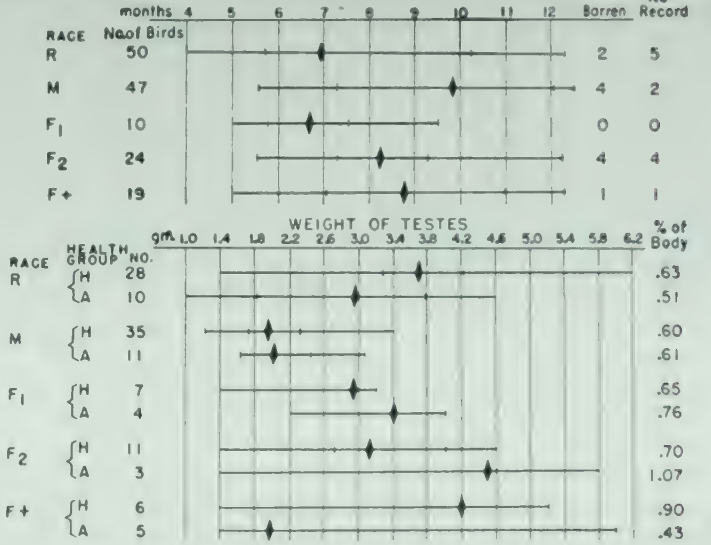


FIG. 149

RUNT AND HOMER C RACES AND THEIR HYBRIDS

AGE AT FIRST OVULATION

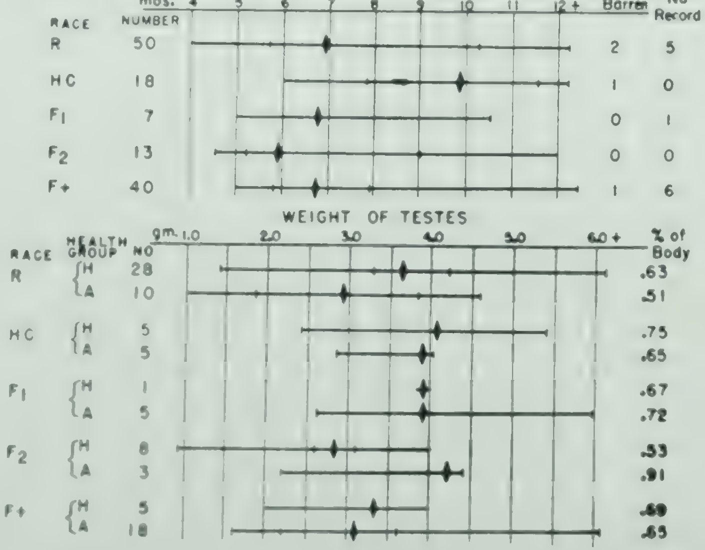


FIG. 150

RUNT AND 299 RACES AND THEIR HYBRIDS

AGE AT FIRST OVULATION

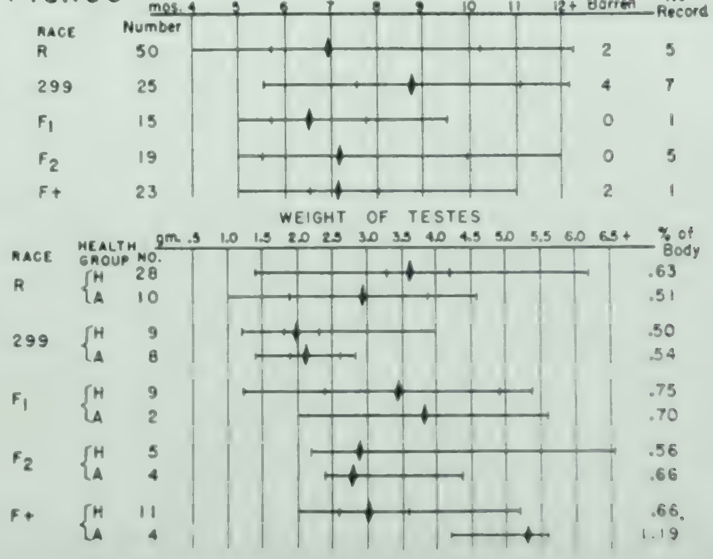


FIG. 151

TIPPLER AND 267 RACES AND THEIR HYBRIDS

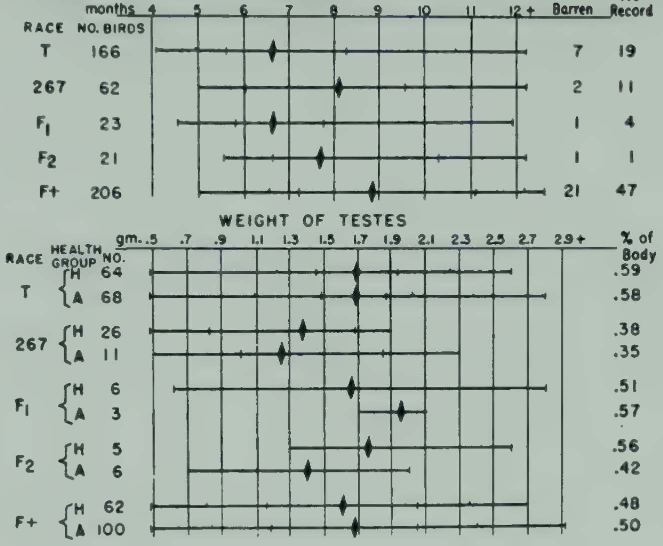


FIG. 152

TIPPLER AND SA-E RACES AND THEIR HYBRIDS

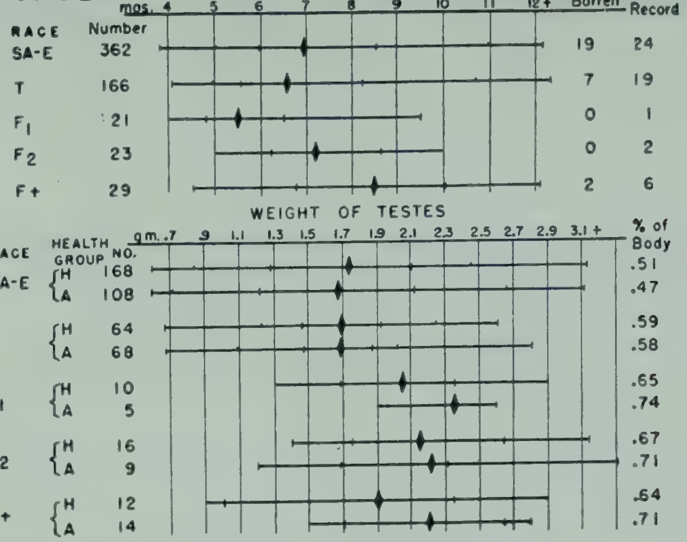


FIG. 153

HOMER AND TIPPLER RACES AND THEIR HYBRIDS

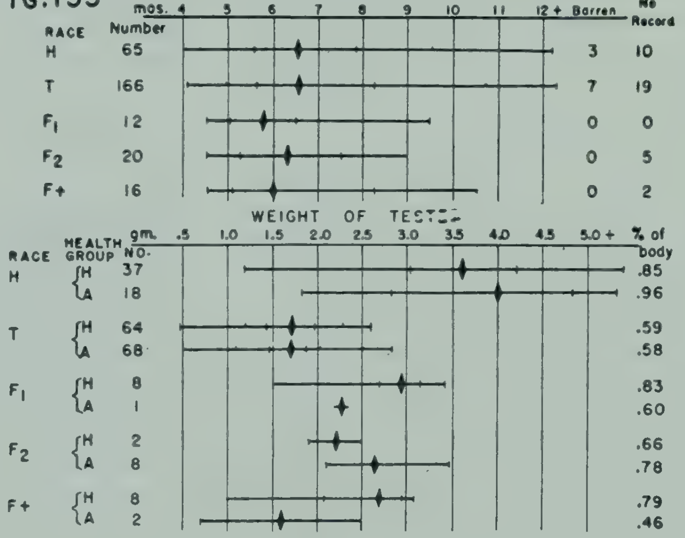
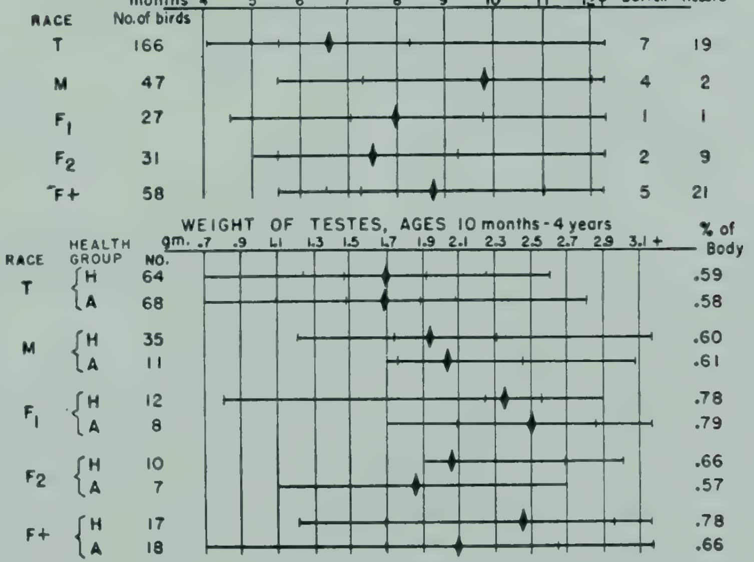


FIG. 154

TIPPLER AND MAGPIE RACES AND THEIR HYBRIDS



The behavior of genetic factors for maturity in 9 types of hybrids is described by analyses given in figures 146 to 154. Quite generally the F_1 showed an earlier median age at first ovulation, a less extended range, and a lower coefficient of dispersion than either parental race. It is especially to be noted that in 7 of the 9 cases the F_1 hybrids matured earlier than the earlier-maturing parent race; in 1 case (*T* × *267*) age at maturity was identical with that of the earlier-maturing parent; and in the remaining case (*T* × *M*) the hybrid value was closer to that of the early-maturing than to that of the late-maturing parent race. Heterosis is thus clearly shown by these tests.

In most instances the F_2 generation showed a return toward parental variability and range, and to an intermediate median. Partial exceptions are observable in hybrids *R* × *M*, *R* × *SA-E*, *R* × *HC*, and *T* × *SA-E;* in the last-named cross the age at maturity was a little later than that found for either parent.

In the F_+ generations (i.e., all later than F_2) there is a general tendency to still later maturity medians; the exceptions here relate to *R* × *HC*, *T* × *H*, and *R* × *299*. Since a high degree of inbreeding was practiced in obtaining most of these F_+ populations, the data seem to warrant the conclusion that in these cases inbreeding tended to increase age at first ovulation; and, more definitely, crossing tended to decrease it. Stated otherwise, the basis of age at maturity is partly a matter of heterosis. It is difficult to decide whether one is warranted in assuming that Magpie and Homer *C* were late-maturing races because of a previous history (largely unknown) of much inbreeding. Moreover, the fact that the F_1 of *M* × *T* (late × early) was intermediate, and the further fact that other F_1 results from crosses involving late-maturing races were in general later than from other crosses,[12] suggest that inbreeding alone does not adequately account for the results; genetic factors more or less specific for maturity seem also to be involved. F_+ of *T* × *267* matured later than either of the parental races. These results on effect of crossing on age at maturity in pigeons are quite comparable to those reported by Dunn[13] and by Warren[14] for fowl.

In some cases, both in doves and in pigeons, the early-maturing races (*63*, *78*, Homers) were also races in which testis size was extremely large; and some late-maturing races (Magpies) had very small testes. Opposite conditions, however, are observed in still other races (*44*, *N2*, and *SA-E*).

Summary

Age at first ovulation (sexual maturity) in female doves and pigeons is affected markedly by season of origin and also by undefined genetic factors. The seasonal factor is less manifest in pigeons than in ring doves.

Some of the pairs of ring doves (or their early progeny) which were selected as the starting point of 24 races produced populations which were predominantly early-maturing races, and other such pairs gave rise to late-maturing and intermediate populations. Races *63*, *44*, and *78* matured early. Races *72*, *51*, *N2*, and *65* were predominantly late-maturing populations.

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[12] The earliest-maturing F_1 were obtained from crosses of early × early.

[13] See footnote 8.

[14] See footnote 9.

Standard (previously established) varieties of domestic pigeons include both early- and late-maturing breeds, and also breeds which apparently have an intermediate age or ages at maturity. Homers and Tipplers matured earlier, and Homers *C* and Magpies matured later, than other breeds studied. Runts and *SA-E* matured only slightly later than Homers and Tipplers.

More definitely in pigeon crosses than in dove crosses, the F_1 showed heterosis, namely, an earlier median age at maturity, a less extended range, and a lower coefficient of dispersion than that found in either parental race.

Age at maturity in the females of a race does not seem to be significantly correlated with testis weight in the males of the race.

The physiological basis of sexual maturity in these animals is known from other studies to rest largely upon the time and extent of output of gonadotrophic hormone by basophilic cells of the anterior pituitary gland. The genetic factors which affect age at attainment of sexual maturity probably act through or upon the basophilic part of the anterior pituitary.

8

TESTIS WEIGHT AS A RACIAL CHARACTER

Preliminary Statement

After the age of 2.5 months (pigeons) or 3.0 months (doves) the weight of testes, like age at maturity in females, is under the immediate control of the gonadotrophic hormone of the anterior pituitary.[1] The output of gonadotrophic hormone, however, can be suppressed experimentally by the administration of another pituitary hormone (prolactin); and probably the normal and cyclic occurrence of excess production of prolactin in the bird's own pituitary likewise results in some diminution of the testes and of the ovary. Thus, in quite healthy males the testes have been observed to diminish in size (about 25 per cent) during the incubation of eggs,[2] and this period is also known (from concurrent growth in the crop sacs) to be a period of increased output of prolactin by the pituitaries of incubating doves and pigeons. One further fact concerning the weight of the "normal" adult testis is especially to be noted here. Such "normal" weights in doves are readily convertible into "supernormal" weights (30 to 60 per cent increase) by ten daily injections of pituitary gonadotrophin.[3] Thus actual testis weight in adults is an expression of the quantity of gonadotrophin which the anterior pituitary is currently releasing to the blood stream.

The two main sources of variability of testis weight in adults are immaturity and disease. At the age of 5 months the testes of two entirely healthy doves might weigh 50 and 500 mg., respectively. This difference would rest on the fact that mere traces of gonadotrophic hormone had yet been secreted by the pituitary of one bird, but much larger amounts of this hormone had been secreted during several days or a few weeks in the other bird; at the age of 8 or 10 months, however, such differences have practically never been observed in healthy birds. Again, the testes of a dead or diseased dove aged 12 months may weigh only 100 mg., whereas all of a dozen healthy doves of that age would have testes weighing between 800 and 1400 mg. For these reasons only testes of healthy doves or pigeons (and those with ascariasis) aged 10 to 48 months have been included in this study. Data from birds older than 4 years are excluded because such birds are not represented in some races or types, and because the effect of extreme old age on testis size is not adequately known. Season has been observed to have a moderate effect on testis weight, particularly in doves;[4] that effect, however, is largely equalized for the various races and types by the fact that data for all types were obtained throughout the year. The two testes provide a single measure of testis weight.

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[1] Riddle, O., and F. Flemion, Amer. Jour. Physiol., 1928, vol. 87, p. 110; Riddle, O., and I. Polhemus, Amer. Jour. Physiol., 1931, vol. 98, p. 121.

[2] Champy, C., and P. Colle, C. R. Soc. de biol., 1919, vol. 82, p. 818; Schooley, J. P., and O. Riddle, Amer. Jour. Anat., 1938, vol. 62, p. 319.

[3] Riddle, O., and R. W. Bates, Endocrinology, 1933, vol. 17, p. 689.

[4] Riddle, O., Amer. Jour. Physiol., 1925, vol. 73, p. 5.

Jaap and Thompson[5] have shown that natal testis size is heritable in fowl. From certain reciprocal crosses they obtained evidence of hybrid vigor and the action of sex-linked as well as autosomal genes on the size of the testes at hatching.

Dove Races and Hybrids

Data for 21 races, and for a few F_1 hybrids, are presented in summary form in a single chart (fig. 155). Several relations, particularly those concerning body weight and percentage of body weight, are shown. The diamond-shaped "frames" which enclose names of races show, by the radial distances from their centers, the probable errors of the medians for both testis weights and body weights. Most median testis weights fall between 0.5 and 0.9 per cent of the body weight; and a similar relation to body weight will later be observed in pigeons. Racial differences are as great among the group of races which are pure *Streptopelia risoria* as among groups which carry some blood of another species or genus.

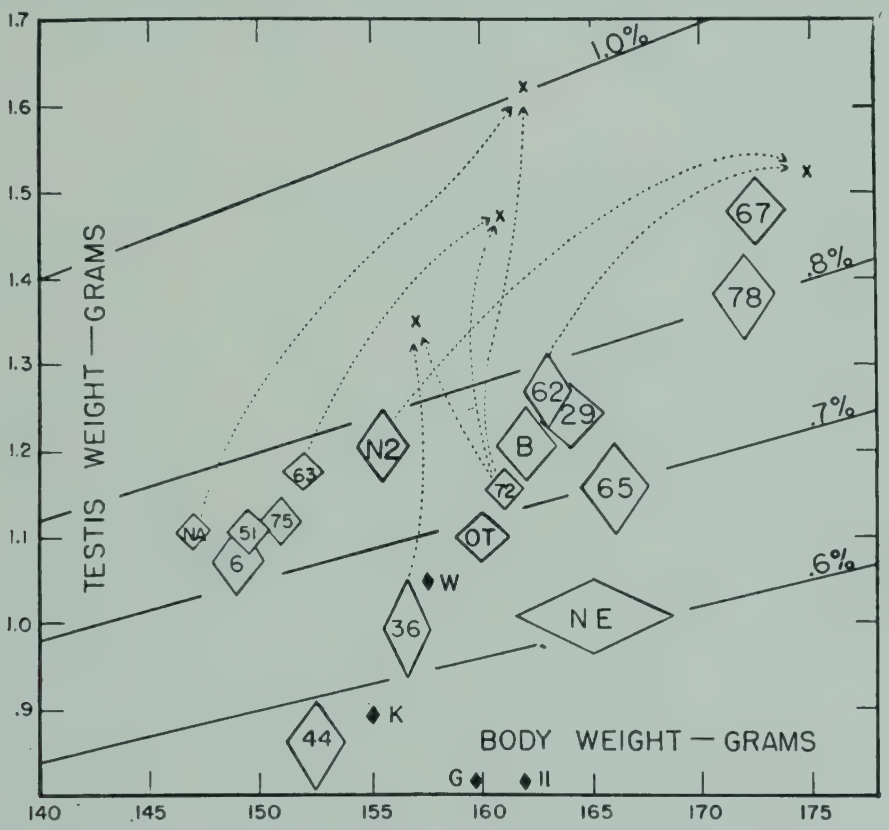

FIG. 155. Showing median testis weight in relation to median body weight in 21 races of doves; dotted lines lead to median testis weights (at *X*) of F1 hybrids of certain races. Vertical extensions of the diamond-shaped frames from their centers represent the probable error (× 1) of the testis weights; horizontal extensions represent the probable error of the body weights.

[5] Jaap, R. G., and R. B. Thompson, Growth, 1944, vol. 8, p. 311.

Unusually large testes characterized races *67*, *78*, and *63* (perhaps *N2* and *62*); extraordinarily small testes were obtained from races *G*, *11*, *44*, *36*, *NE*, and *K*. Coefficients of dispersion are quite similar to those for pigeon races, except for the group of races whose testis weights were very low. In these last-named races the coefficients of dispersion are much higher—up to 0.7 in the case of race *G*. It is possible that these very high coefficients of dispersion reflect an unrecognized pathological condition in these races, and that this pathology in turn was responsible for the extremely low position of these races in the scale.

In the F_1 crosses there is a marked tendency to relative and actual increase of testis weight. Data for only 4 such crosses are indicated on the graph. Fairly large numbers were available for these particular crosses, and the results obtained for them are representative of results for the uncharted hybrids. Coefficients of dispersion for testis weight in the hybrids are very similar to those for the respective parent races.

Two of the preceding results are especially to be noted. It is interesting that heterosis is so strongly manifest in testis weight (males), but much less so in age at maturity (females). In view of the marked effect of state of health on testis size, it is possible that heterosis increased testis size partly or mainly through improved health. Again, it is remarkable that relative testis weight in the different races does not appear to be significantly correlated with age at maturity in the females of the same races. Granting that the two phenomena are governed by output of basophilic cells of the pituitary, it might be assumed that age at maturity in females reflects the *time* of this output, whereas testis size (as measured here) reflects the *persistence* of this output. The genetic factors here, irrespective of their place or mode of action, are apparently different and more numerous for the control of testis weight (persistence) than for age at maturity (time). The evidence that different factors are involved is provided by the observed lack of correlation between testis size and age at maturity. That more numerous factors are involved in the control of testis weight is indicated by the heterosis evident in testis weights for F_1 hybrids and the lack of heterosis in the case of age at maturity. The fact that heterosis was not observed in testis weights obtained from crosses of most pigeon races does not affect the validity of this conclusion regarding the situation in ring doves.

Pigeon Races and Hybrids

Survey data for 11 pigeon races and several hybrid types are charted (fig. 156) in the form earlier used for doves. The data indicate that races *267*, *S.A-E*, and *299* had unusually small testes. In race *H* (our own Homers) the testes were exceptionally large. Tipplers (*T*), Magpies (*M*), and Carneaux (*C*) had relatively small testes.

Percentile analyses of testis weights are also given for 10 races (figs. 144, 145). Coefficients of dispersion are lowest (about 0.13) for Tipplers and highest (about 0.27) for race *S.A-E* (normal type only). These two races do not show very large differences in body weight. There is no consistent tendency to skewness of dis-

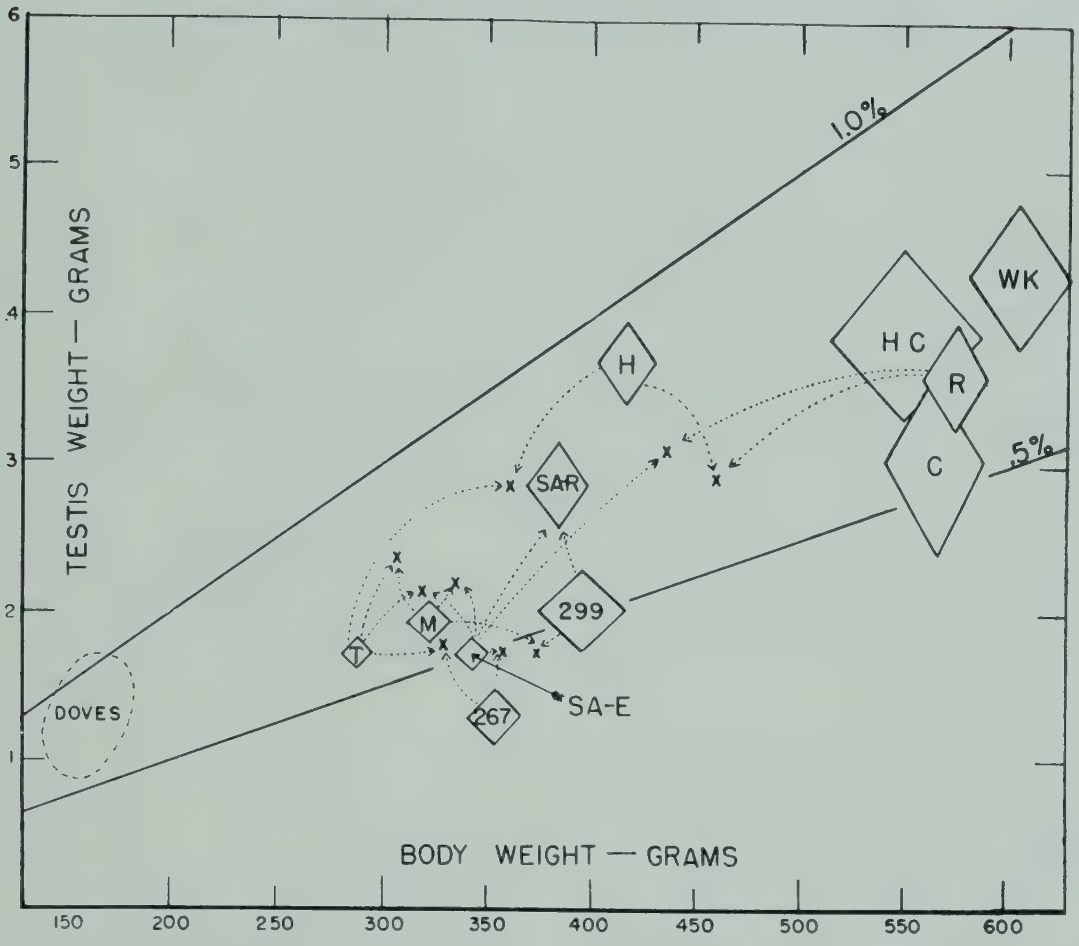

FIG. 156. Showing median testis weight in its relation to median body weight in 11 pigeon races. Dotted lines are used to indicate the crosses made; *X* marks points of median testis weights of F1 hybrids from these crosses. Dotted lines (not ending in an *X*) lead from *SA-E* and *299*, and end near *SA-R;* this indicates that *SA-R* is a derivative, but not really F1, of races *SA-E* and *299*. Vertical extensions of the diamond-shaped frames from their centers represent 3 times the probable error of the testis weights; horizontal extensions of these frames represent 3 times the probable error of the body weights.

tribution of testis weights. In these analyses testis size is plotted for only healthy (H) and *Ascaridia*-infested (A) birds. A significant difference between the two groups is found only in Runts (*R*) and White Kings (*WK*); but since the direction of the difference is not the same in the two cases, this difference apparently has no recognizable meaning.

Increased testis weight, both actual and relative to body weight, was observed in the F1 of 2 crosses, *T* × *M* and *T* × *SA-E* (figs. 154, 152). Otherwise, testis weight in F1 either was nearly intermediate or showed a slight relative increase. It is interesting to note that the cross which here gave more obvious heterosis, *T* × *M*, did not show heterosis for age at first ovulation. On the other hand, *T* × *SA-E* showed heterosis for testis weight, for age at first ovulation, and for weight of eggs. Two crosses, *R* × *H* and *R* × *M* (figs. 146, 148), show a tendency to increased relative testis weight in F_2. All other crosses show a tendency to decreased testis weight in F_2, though the tendency is not very marked. In *T* × *S.A-E* hybrids (fig. 152), the heterosis effect is observable in the F_2 to practically the same extent as in F_1. In comparison with the parental races, the coefficients of dispersion do not show much reduction in F_1 or much increase in F_2. This fact, like others already observed, apparently indicates a considerable influence of environmental factors on the variability of testis weight. Percentile analyses of testis weight in 9 hybrid types are given in figures 146 to 154; a comparison of testis weight with age at maturity is thus facilitated.

It seems more than mere coincidence that the lowest testis weights (median and general distribution as well as relative to body weight) are found in race *267*, the race in which a case of true hermaphroditism first appeared. The testes of birds of this race were practically of the same size as those of normal ring doves whose body weight is only one-half that of race *267*. A strain, or race, carrying genetic factors for hermaphroditism was obtained by crossing a female of race *267* with a male Tippler (fig. 151). The resulting hybrids (*T* × *267*) have been selected and inbred and, from one standpoint, are regarded as a separate "hermaphrodite-producing race."

Testis Weight in Immature Doves in Relation to Race

An earlier study[6] showed that the testes of doves and pigeons remain surprisingly small until adult body weight is almost attained. Specifically, the average weight of 10 pairs of testes of doves aged 2.3 months (from egg; 1.8 months from hatching) was 6.56 mg.; this was only 1/175 of the average weight of the testes of birds (110) 1 year old. The body weight of the young birds, however, was exactly 95 per cent of that of the older group. Other measurements made in that study showed that the testes of doves increase very little within the age period 2.0 to 3.0 months, though soon thereafter the testes of most doves begin a surprisingly rapid increase in weight. During several years this laboratory utilized the relative constancy of testes of doves aged 2.0 to 3.0 months as a means for the assay of the gonadotrophin contained in various extracts of anterior pituitary tissue. Indeed, it was in the course of such assays, and in accompanying controls, that we first observed that immature doves of race *W* had unusually large testes and that young doves of race 72 had abnormally small testes. Those observations led to the collection of the additional data which are presented here.

The distribution of testis weights from 4 types of doves aged 2.0 to 3.0 months is shown in figure 157. Only 15 suitably aged individuals of race *W* were available for measurement, but it is clear that testis weight in this race was significantly different from that in the other 3 populations. The average age of the birds used in this group was 2.6 months and the weight of their testes was 12.61 ± 1.21 mg. These values for race 72 (43 individuals) were 2.6 months and 4.48 ± 0.18 mg. Twenty-one individuals of race *63*, aged 2.5 months, had an average testis weight of 7.99 ± 0.34 mg. In order to study the behavior of this character in

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[6] Riddle, O., Amer. Jour. Physiol., 1928, vol. 86, p. 248.

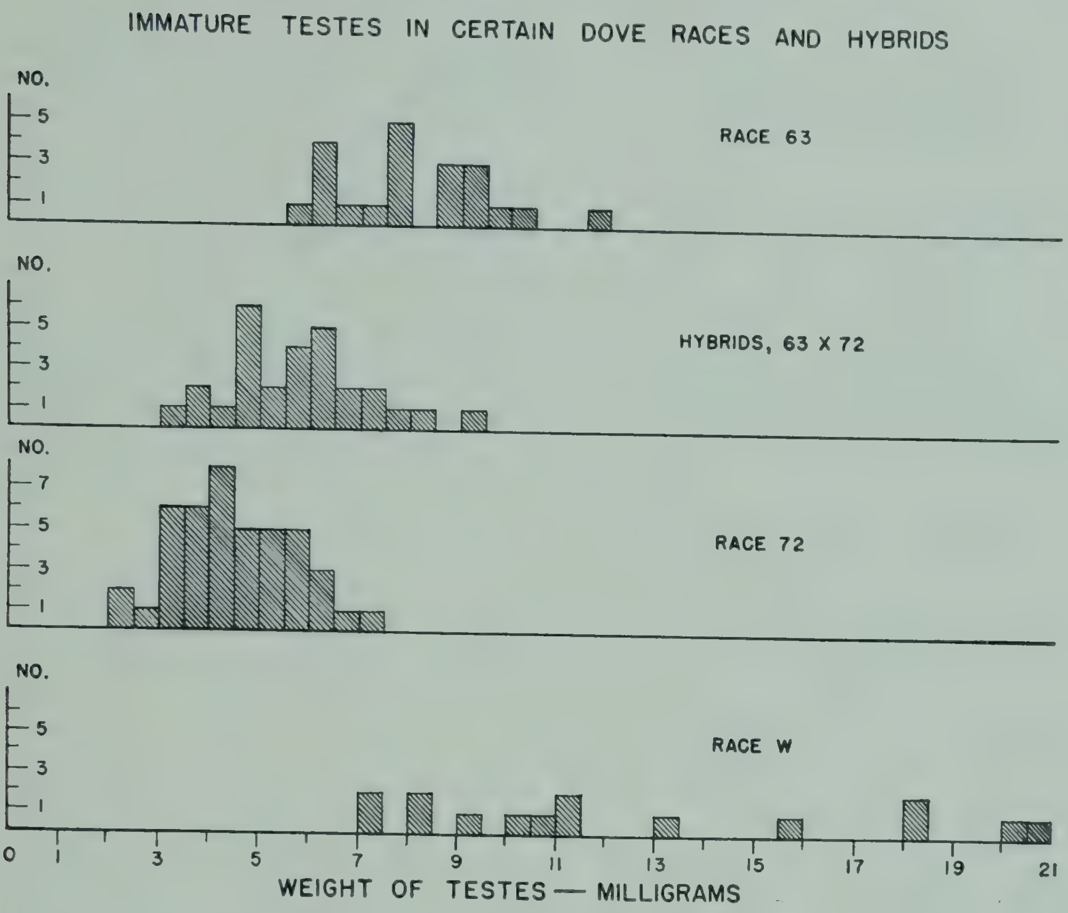

FIG. 157. Polygons showing distribution of weights of pairs of testes of ring doves, aged 2.0 to 3.0 months (from egg; 1.5 to 2.5 months from hatching), and belonging to 3 races and 1 type of hybrid.

crosses, 28 testes of hybrids from races 72 and 63 were obtained. The average age of this group was 2.5 months and average testis size was 5.71 ± 0.26 mg. This value is intermediate to, and significantly different from, the values found for the two parent races. Additional data obtained in assay tests, and less extensive control data from birds aged 3.1 to 3.5 months, fully confirm the conclusion that testis weight was extremely high in race *W* and extremely low in race 72.

Gonadotrophin secreted by the anterior lobe of the pituitary is well known to induce the later growth of the gonads of both sexes. It would seem, therefore, that the simplest explanation of the racial differences in the young birds just discussed would involve nothing more than the beginning, under genetic control, of output of gonadotrophin at distinctly different age levels. A full discussion of this point will not be attempted here, but it will be noted that although size in these immature testes has been shown to be under genetic control, there are some reasons for questioning the view that gonadotrophin is an intermediary in that control. Data of Riddle and Schooley[7] make it appear improbable that the pituitaries of doves such as those of race *63*, at the age of 2.0 or 2.5 months, contain or produce any gonadotrophin whatsoever. Nevertheless, our data indicate that even prior to that age the testes of such birds are distinctly heavier than those of race *72*.

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[7] Riddle, O., and J. P. Schooley, Proc. Soc. Exper. Biol. and Med., 1935, vol. 32, p. 1610; Schooley, J. P., and O. Riddle, Amer. Jour. Anat., 1938, vol. 62, p. 319.

SUMMARY

Median testis weight in essentially healthy adult doves and pigeons usually represents 0.5 to 0.9 per cent of the body weight.

Dove races *67*, *78*, and *63* had relatively high median testis weights; races *44*, *G*, *11*, *K*, *36*, and *NE* had very low testis weights. Whether the observed differences between the extremes of testis weight in adults have a genetic significance seems to rest less upon the size of probable errors of the medians than upon the unanswerable question whether unrecognized disease was prevalent in the races showing abnormally low testis weight. Among the latter races, coefficients of dispersion are higher (up to 0.7) in race *G* than in other races.

If prevalent unrecognized disease was not the cause of consistent depression of testis weight in several or most dove races, the selection procedures practiced in the foundation of these races resulted in the isolation of some races with genetically determined large and small testis size. Such genetic control would probably be exercised through regulation of the output of gonadotrophin by basophilic cells of the pituitary gland.

In F_1 hybrids between dove races, heterosis is strongly expressed in testis weight, but is not evident in age at maturity in the corresponding females. Again, relative testis weight in the various races does not seem to be significantly correlated with age at maturity in the females of the same races. This lack of correlation, though unexpected, is not inconsistent with the view that both testis weight and age at maturity are controlled genetically through the basophilic cells of the anterior pituitary.

Racial differences in median testis size are as great among dove races derived from pure *Streptopelia risoria* as among races with admixture of another species (*St. douraca*) or genus (*Turtur orientalis*).

Exceptionally large testes were found to be characteristic of Homer pigeons. Tipplers, Magpies, and Carneaux had relatively small testes, and races *267*, *SA-E*, and *299* had extremely small testes. It is wholly improbable that masked disease, or another environmental factor, was responsible for small testis size in these 6 races.

In the testes of F_1 hybrids, heterosis was found in only 2 of 10 tests. The hybrid (*T* × *M*) which showed most obvious heterosis did not show heterosis for age at first ovulation; the other one (*T* × *SA-E*) showed heterosis for testis weight, for age at first ovulation, and for weight of eggs.

The observed heterosis (doves chiefly) indicates that multiple factors are involved in control of testis weight.

Race *267* had the lowest median testis weight observed among a total of 11 pigeon races and 9 hybrid types subjected to study. It was this race that gave rise to a case of true hermaphroditism, and from which (in a cross with Tipplers) a strain or race carrying factors for hermaphroditism was developed.

In juvenile stages, presumably prior to production of gonadotrophic hormone by the pituitary, dove race *72* was characterized by abnormally small testes; race *63* by testes of medium size; and race *W* by unusually large testes. In the adult stage races 72 and *W* had testes of essentially normal and nearly equal size; adults of race *63* had unusually large testes.

From the pairs of birds of pure *St. risoria* stock which were selected to found several races of ring doves, probably three distinct genetic combinations affecting size of the immature testis were isolated in races *72*, *63*, and *W*. Nothing is known of the number of genetic factors concerned, and participation of pituitary gonadotrophin in establishing these unequal levels of early testis growth is doubtful.

9

EGG WEIGHT AS A RACIAL TRAIT

HISTORICAL

Most eggs laid by doves and pigeons were weighed within 1 to 4 hours after laying; other eggs were weighed after a slightly greater delay. In these species, as in poultry in general, it is well known that the eggs laid over a period of time by any particular female are far from uniform in weight. Indeed, this variation is so great, and its environmental causes are so numerous, that the question of the existence of a "norm" for either the individual or the race requires special study.[1] So far as the individual dove or pigeon is concerned, it can be said that such a study clearly indicates a tendency for the weights of the several eggs of different females to vary around different norms. The extent to which egg weight varies among individual females is not, however, the subject of the present chapter.

Studies on the inheritance of egg weight seem previously to have been made only on fowl.[2] Those studies were concerned almost exclusively with intra-breed differences and they are thus not precisely comparable with the data considered here. Heterosis in regard to egg weight has not previously been seriously investigated; the present data indicate, however, that it may be of importance in some crosses.

The females that contributed data to the present study laid very unequal numbers (4 to more than 100) of eggs. It was decided to take the average of the first 4 eggs laid (see below) by a bird as one measurement of egg size for that bird; and if this bird laid additional eggs (4 to 100), to use also the average of the last 4 eggs as a second and independent measurement. If fewer than 8 were laid, the first 4 alone were averaged. Casual examination of the distributions of averages thus obtained in various races clearly showed that the first 4 eggs were usually smaller than later eggs, and that as in poultry this tendency was especially evident for birds which began laying while very young. Consequently, the average of the first 4 eggs was not accepted for any bird which produced these eggs before she was 7 months old. It follows from the above explanation that there are more egg-weight determinations than there are females (about 1.5 per female). The several accepted averages for all the birds of a race were put into a frequency distribution and the data analyzed by the percentile method. Although entirely accurate data (for the weight of eggs produced by an individual bird) were rarely obtained, it seems probable that these inaccuracies have had little effect on the median values obtained for the several races. Possibly the values obtained for a few early-maturing races were somewhat increased through our rejection of weights for first eggs laid by birds less than 7 months old.

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[1] Hadley, P. B., and D. W. Caldwell, Rhode Island Agric. Exper. Sta. Bull. 181, 1920; Bennion, N. L., and D. C. Warren, Poultry Sci., 1933, vol. 12, p. 69.

[2] Hays, F. A., Poultry Sci., 1941, vol. 20, p. 217.

Data for Dove Races and Hybrids

The relation between egg weight and body weight of the egg producer is of much importance; and this is true even when the difference in body weight, as among dove races, is not very great. This relation is fairly evident in the chart (fig. 158), which permits a summary view of data for egg weight in 14 dove races and several types of F_1 hybrids. This chart further shows that races 75 and *NE* (also hybrids 75 × 72 and 72 × *NA*) produce eggs which are quite heavy in relation to body weight; in all these groups egg weight equals or exceeds 5.5 per cent of the body weight. Races *44* and *N2*—the two races which elsewhere are observed to show extreme length of intestines—produced the smallest eggs (4.7 and 4.8 per cent of body weight, respectively).

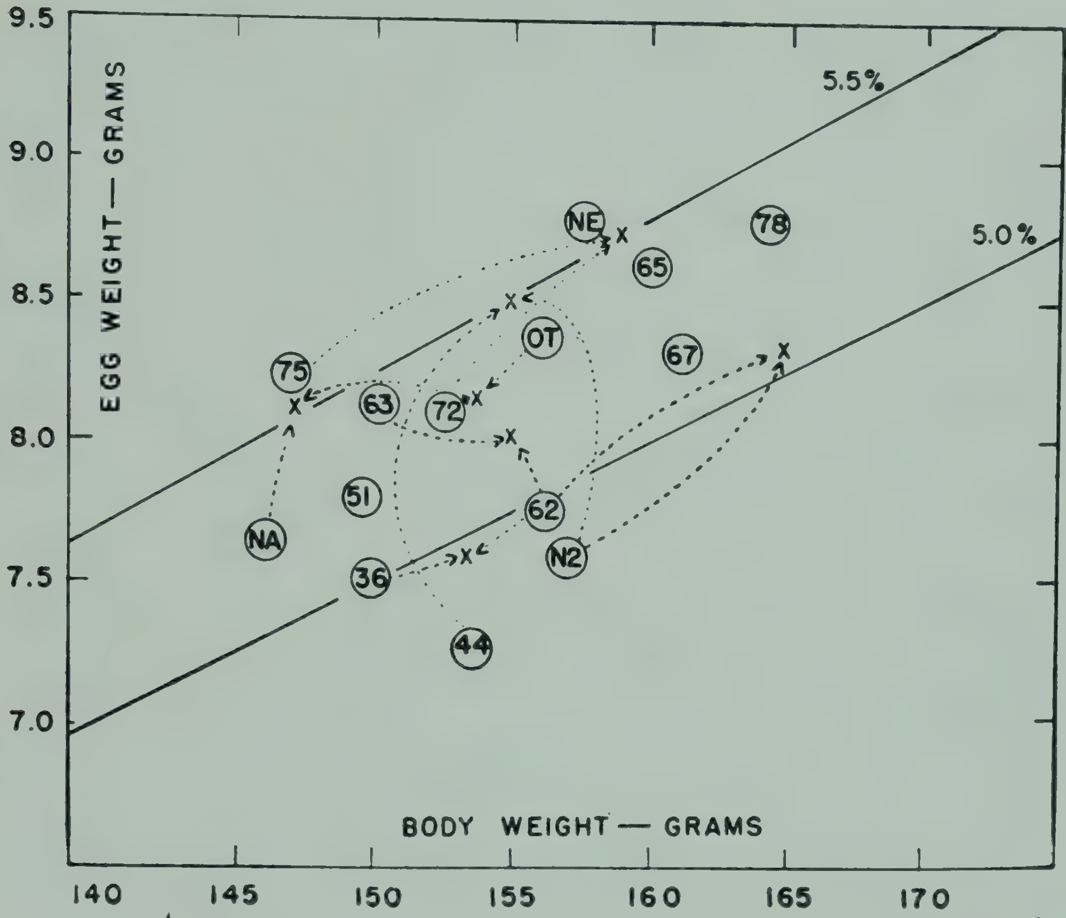

Fig. 158. Egg weight in relation to body weight in 14 dove races and in several types of their F1 hybrids (represented by *X*).

Percentile analyses of data for 20 dove races, and for the 7 most numerous types of hybrids, are given in figure 159. It will be noted that the distributions show no definite tendency to skewness. Coefficients of dispersion vary from about 0.15

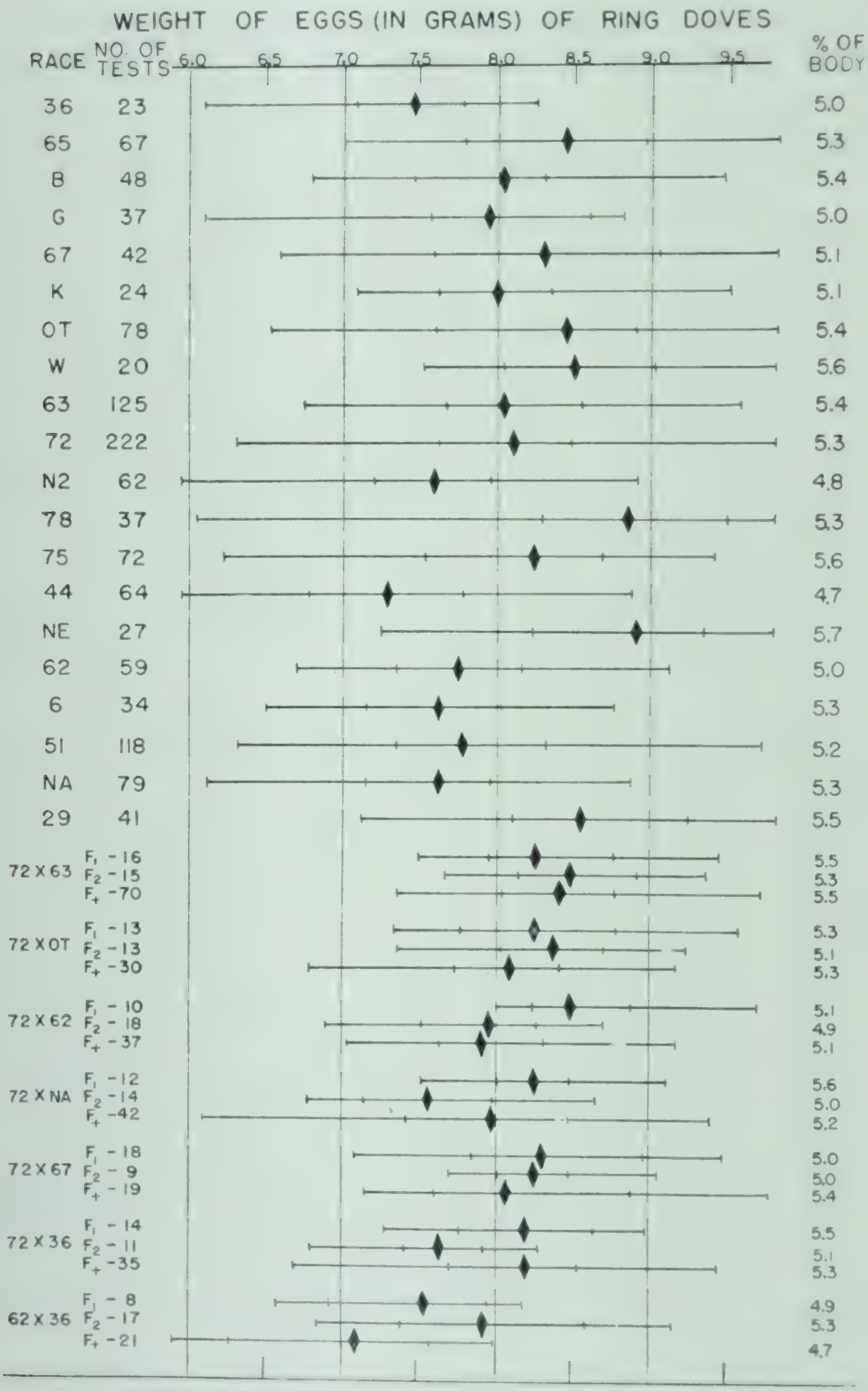

FIG. 159. Percentile analyses of data for egg weights obtained for 20 dove races and for 7 types of dove hybrids.

for race *N2* to about 0.8 for race *OT*. It is necessary to remember, however, that these coefficients apply to averages of 4 eggs, not to single egg weights, for which coefficients and ranges would be much greater. These data indicate that race *W* produced unusually large eggs (5.6 per cent of body weight); also that race *63* belongs in the group of races which produced large eggs (5.4 per cent of body weight). The data further show that races *G*, *36*, and *62* (and *62* × *36* hybrids) produced eggs somewhat smaller (5.0 per cent of body weight) than those of most dove races. Races which are pure *Streptopelia risoria* therefore tend to show the same differences in egg weight which are shown by the races which contain the blood of another species or genus.

It should next be noted that egg weight was relatively high in the 3 particular females which founded the 3 populations (*NE*, *75*, and *W*) showing highest egg weight; in these 3 females egg weight averaged 5.2 per cent of body weight. Similarly, the 3 females which founded the 3 populations (*44*, *N2*, and *62*) showing lowest egg weight produced eggs which averaged 4.8 per cent of their body weight. The same calculation was made for 3 females which founded large populations (*72*, *51*, and *OT*) whose egg weights were of intermediate size; their average egg weight was 4.7 per cent of their body weight.

The F_1 hybrids from dove races usually had egg weights intermediate to those of the parent species. Hybrids of 2 types, *N2* × *44* and *NA* × *72*, were exceptions which showed marked increases in egg size. Percentile analysis for the *N2* × *44* hybrids was omitted, however, because of the small number of tests. In F_2 hybrids, both in doves and in pigeons, egg weight tends to decline slightly from the level found for F_1.

The data accepted and presented here indicate that the two racial traits egg weight and age at maturity are not correlated. It is again noted that our rejection of weights of eggs produced before the seventh month of the bird's life would tend to minimize or obscure that correlation if it existed in early-maturing races; but lack of correlation is also indicated by the fact that late-maturing races (*72*, *NA*, *N2*, and *75*) show both high and low median egg weights (5.3, 5.3, 4.8, and 5.6 per cent, respectively). Races *44* and *78* both matured early, but they differ markedly in egg weight; again, races *72* and *63* differed greatly in age at maturity, but their egg weight relative to body weight is almost identical.

Again, egg weight in dove races is not clearly or strongly correlated with testis size. Races *75* and *NE* produced the largest eggs; but testis size was greater in *75*, and less in *NE*, than the average for other dove races. Likewise, the races having lowest egg weight were *44* and *N2;* but testis size was greater in *N2*, and less in *44*, than the average for other dove races.

Data for Pigeon Races and Hybrids

A survey chart (fig. 160) for pigeon races and hybrids indicates an increase in egg weight roughly in proportion to the ascending order of body weight. In addition, however, it is quite clear that the egg size of the larger races represents a somewhat lower percentage of the body weight. This same principle or tend-

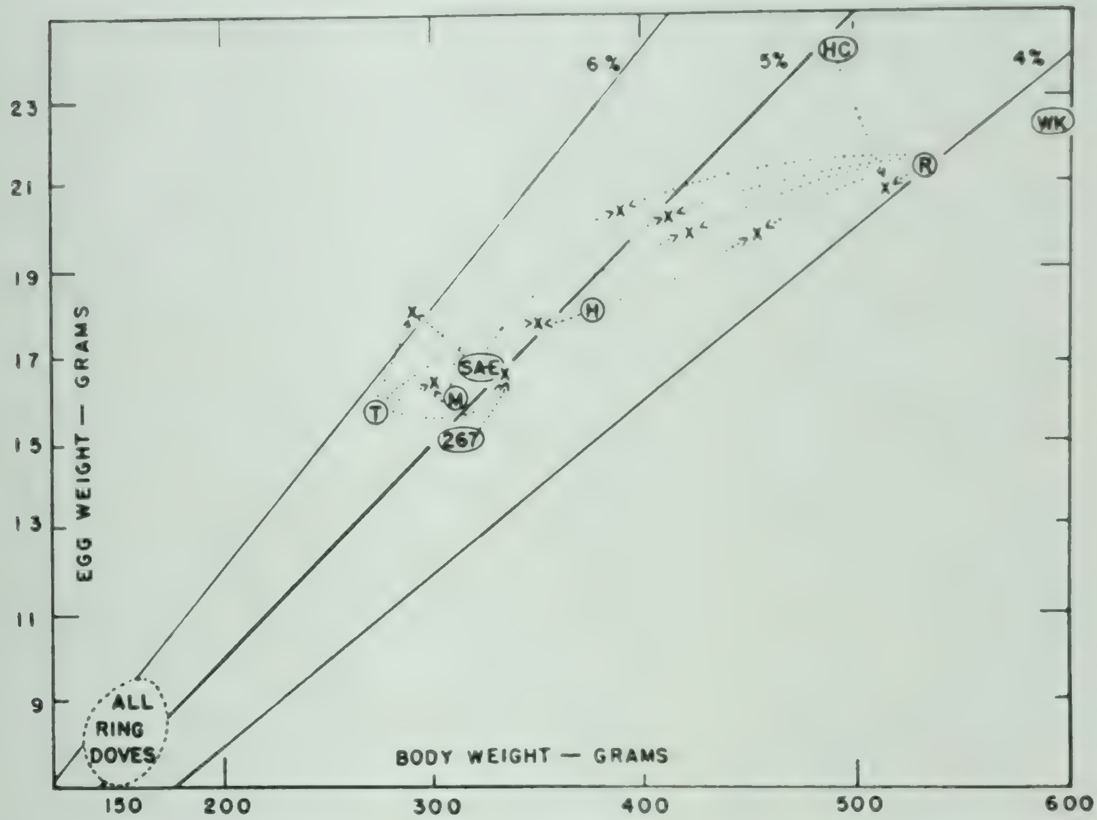

FIG. 161. Percentile analyses of data for egg weights obtained for 11 pigeon races and F_1 hybrids (represented by *X*).

ency is well known to exist in the various kinds of birds; in other words, in the largest birds (ostrich, turkey, fowl) egg weight represents a smaller proportion of body weight than in birds of intermediate or small size.

Line analyses for 11 pigeon races and for 10 types of hybrids are given in figure 161. Coefficients of dispersion for these races vary from about 0.05 in the Tipplers to about 0.1 in the Carneaux. The distributions show no definite tendency to skewness. In F_1 from crosses between pigeon races in which relative egg weight differs markedly, the value obtained was more or less intermediate. F_1 of the *T* × *SA-E* type, however, had particularly high egg weight—both actually and relatively higher than that of either parent race. This case provided the most outstanding item of evidence for heterosis obtained in this species. In F_2 hybrids generally, the data indicate a tendency toward a slight decrease in relative egg weight as compared with F_1; an apparent exception is indicated by the relatively few measurements made on *R* × *HC* hybrids.

SUMMARY

The average weights obtained from the first and last 4 eggs laid by a female dove or pigeon were regarded as a measure of egg size for that female. Such measurements of egg weight were analyzed by the percentile method.

With differences in body size fully recognized, egg weight was exceptionally

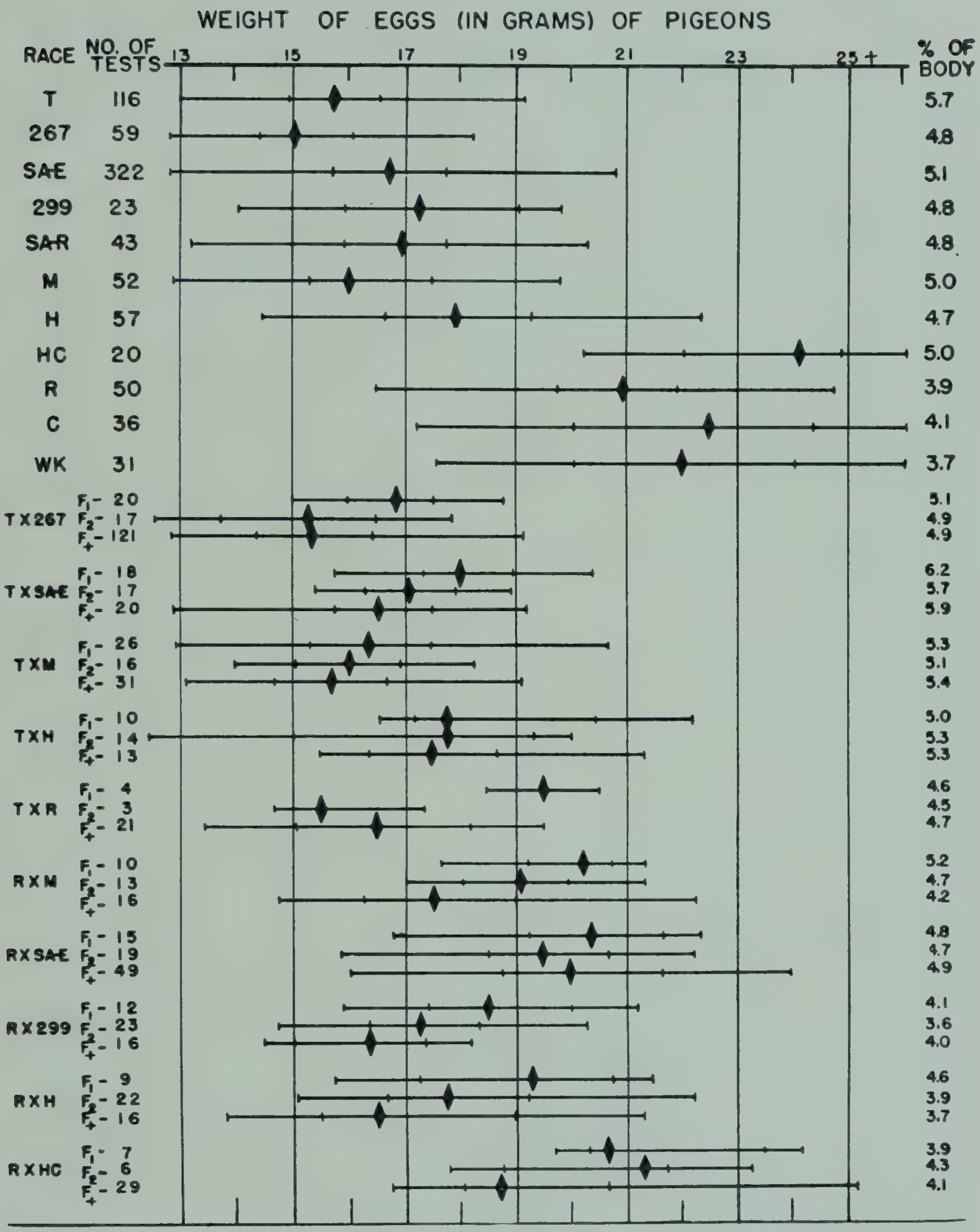

FIG. 161. Percentile analyses of data for egg weights obtained for 11 pigeon races and for 10 types of pigeon hybrids.

large (5.5 to 5.7 per cent of body weight) in dove races *75*, *NE*, *W*, and *29;* and in hybrids *75* × *72* and *72* × *NA*. Exceptionally low egg weight (4.7 and 4.8 per cent of body weight) characterized races *44* and *N2;* and these particular races are elsewhere found to have the greatest length of intestines observed in ring doves. Other races showing relatively low egg weight (5.0 per cent of body weight) were *62*, *36*, and *G*.

Variation in egg size was as great among races containing only *Streptopelia risoria* as among races containing some blood of another species or genus.

The selection procedures involved in the foundation of these dove races resulted in the separation of types (races) having characteristically higher and lower egg weight. Egg size averaged 5.2 per cent of the body weight in the 3 females which served as starting point for the 3 races which showed highest egg weight; the average was 4.8 per cent of the body weight in the 3 females which served as starting point for the 3 races which showed lowest egg weight.

The F_1 hybrids from dove races usually showed egg weights intermediate to those of the parent species. In 2 hybrid types, *N2* × *44* and *NA* × *72*, egg size apparently exceeded the value found in either parent.

Among the smaller races of pigeons, egg size is relatively greater in Tipplers than in Magpies and race *267*. Among larger pigeon races, egg size is relatively greater in race *HC* than in Runts, Carneaux, and White Kings.

In F_1 hybrids from pigeon races, egg weight was usually intermediate to that of the parent races. In *T* × *SA-E* hybrids egg weight was greater than in either parent. Data for F_2 hybrids indicate a tendency toward a slight decrease from weights observed in F_1.

10

A RACE OF HERMAPHRODITE-PRODUCING PIGEONS

A case of hermaphroditismus verus appeared in the seventh generation of race 267. A sister of this affected individual was mated to a male of another breed (Tippler) and produced hermaphrodites in F_1. The several later generations of the descendants of this pair have produced some true and many pseudohermaphrodites as well as normal females and a low percentage of normal males. Most of the true hermaphrodites have been fertile, at least temporarily, as males. Fairly complete information concerning the parentage and relationships of many individuals of both intersexual types is given in figure 162, below.

Literature on Hermaphrodite Strains

The present chapter is concerned chiefly with, first, the endocrine and genetic elements which accompany the hermaphrodite condition; and, second, a brief comparison of certain constitutional elements (testis weight, heat production, etc.). A preliminary report[1] has noted the establishment of this strain, and another study[2] has supplied the histological data and other details which provide an anatomical characterization and a partial genetic analysis of these deviations from normal sexuality. Those reports have shown that in the true hermaphrodites the typical condition is as follows: On the left side, an ovotestis with the ova relatively little developed; oviduct complete and, in adults, enlarged or even functional. On the right side, a testis somewhat or much smaller than normal; oviduct absent or traces only. Two vasa deferentia are usually present but the left is likely to contain no sperms. Pseudohermaphrodites have apparently normal (rather small) testes on both sides, but they have a left oviduct which varies greatly in development.

A strain of Drentisch fowls, bred in Holland for some years by Houwink, was perhaps somewhat similar to the present strain. Five specimens of Houwink's birds were examined by Boring and Pearl and regarded by them as hermaphrodites;[3] it should be noted, however, that only one of those five specimens can be regarded as a true hermaphrodite, and additional data—perhaps available in Holland—are necessary to establish the inheritance of hermaphroditism in these birds. The very few hermaphrodite fowls studied by Boring and Pearl were regarded as genetic females. Rather clearly, however, the hermaphrodites of the present strain of pigeons are genetic males.

The fact that pseudohermaphroditism (very few recorded cases of true hermaphroditism) is inherited in Toggenburg and Saanen goats has been well established by Crew[4] and by Eaton and Simmons.[5] Male pseudohermaphroditism in man has been shown to appear repeatedly in certain families.[6] The anatomical features of various types of hermaphroditism in man have been fully described by Young.[7] Strains of hermaphrodites have been established and studied in *Drosophila simulans*,[8] *D. virilis*,[9] and *D. pseudoobscura*.[10]

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[1] Riddle, O., and J. P. Schooley, Carnegie Inst. Wash. Year Book no. 35, 1936, p. 55; Riddle, O., H. H. Dunham, and J. P. Schooley, Genetics, 1942, vol. 27, p. 165.

[2] Riddle, O., W. F. Hollander, and J. P. Schooley, Anat. Rec., 1945, vol. 92, p. 401.

[3] Boring, A. M., and R. Pearl, Jour. Exper. Zool., 1918, vol. 25, p. 1.

Genetic and Endocrine Factors Involved

The data given in figure 162 provide essential information concerning the stock in which this trait is exhibited in each generation. Some additional facts are given in the publication earlier cited, and the following pages consider the question of the extent to which this trait is controlled genetically.

It is of first importance to know whether the hermaphrodites are genetic males, females, or neither. Three kinds of evidence obtained within the race all indicate that the hermaphrodites are modified genetic males. First, this stock carries two sex-linked factors for plumage color, "ash-red" and "dilution," and their wild-type alleles. In all the numerous hermaphrodites and pseudohermaphrodites whose colors permitted a decision, two alleles have been demonstrated; that is, they were of male genotype. These observations do not exclude the possibility that a sex-chromosome deficiency or deletion is involved; the existence of such a deficiency, however, would be expected to have a harmful, or even lethal, effect in the female as well as in the homozygous male, and such harmful effects seem not to exist. Second, the number of true female offspring obtained slightly exceeds the combined number of males and hermaphrodites. This sex ratio of course suggests that the hermaphrodites arise within the group of expected males. Third, the aberrant state of the hermaphroditic left gonad and left oviduct is similar to the condition which Riddle and Dunham[11] were able to induce in genetic male offspring of ring dove mothers suitably injected with estrogen.

The analysis of results obtained from reciprocal outcrosses of this (*T* × *267*) stock is informative.[12] When hermaphrodites (i.e., modified males) are used in outcrosses, the condition is apparently never expressed in F_1. On the other hand, outcrossed *T* × *267* females produced a high proportion of males with oviducts (pseudohermaphrodites). These results are not readily accounted for on

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[4] Crew, F. A. E., Brit. Goat Soc. Year Book, 1923, p. 61.

[5] Eaton, O. N., and V. L. Simmons, Jour. Hered., 1939, vol. 30, p. 261; Eaton, O. N., Amer. Jour. Veterinary Res., 1943, vol. 4, p. 333.

[6] Pettersson, G., and G. Bonnier, Hereditas, 1937, vol. 23, p. 49; Moebius, H., Ztschr. f. menschl. Vererbungs- u. Konstitutionsl., 1935, vol. 19, p. 456.

[7] Young, H. H., Genital abnormalities, hermaphroditism and related adrenal diseases (Williams & Wilkins Co., Baltimore, 1937).

[8] Sturtevant, A. H., Genetics, 1921, vol. 6, p. 179.

[9] Lebedeff, G. A., Genetics, 1939, vol. 24, p. 553.

[10] Dobzhansky, Th., and B. Spaasky, Proc. Nat. Acad. Sci., 1941, vol. 27, p. 556.

[11] Riddle, O., and H. H. Dunham. Endocrinology, 1942, vol. 30, p. 959.

[12] See footnote 2.

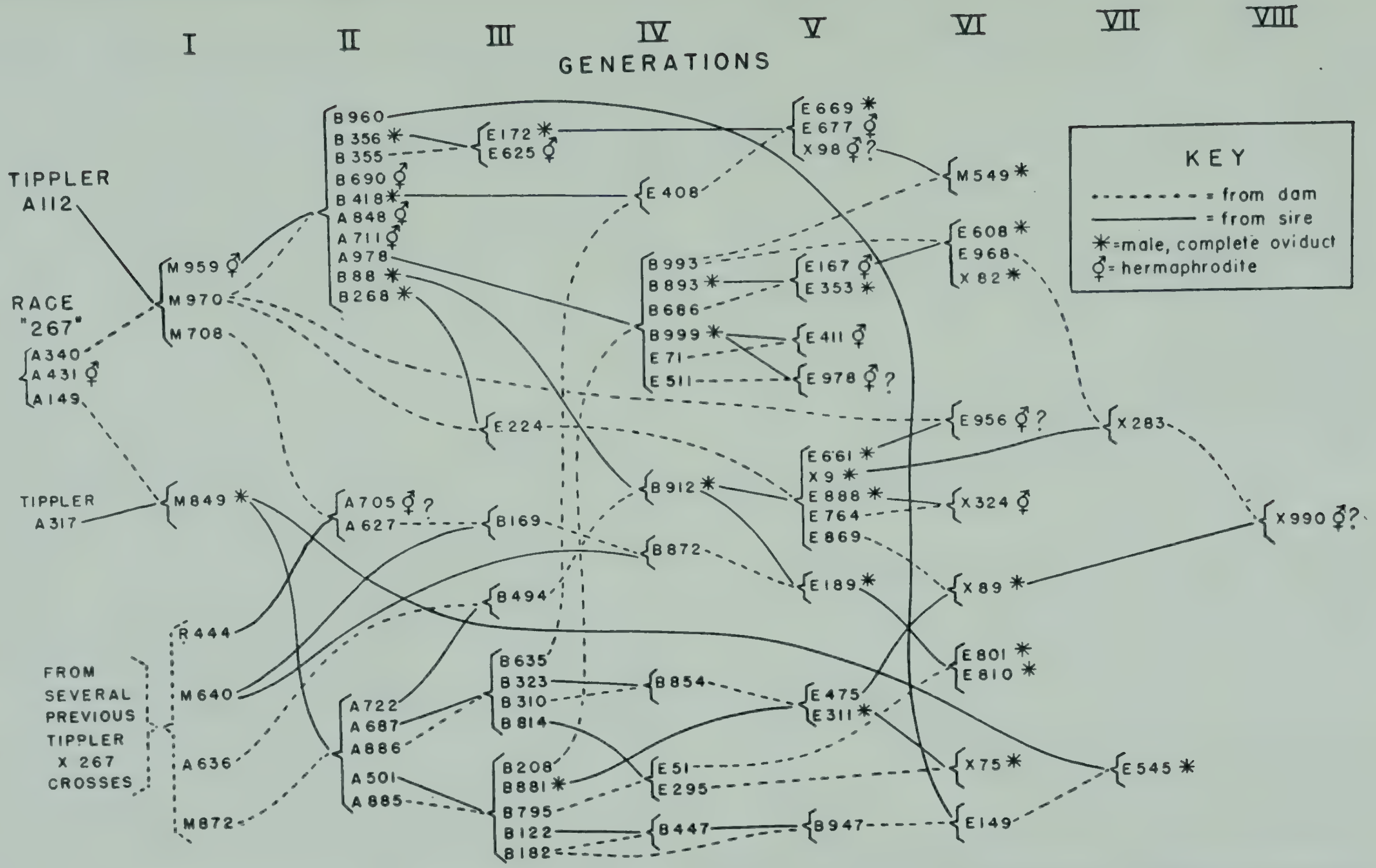

Fig. 162. Showing the existence of true hermaphroditism in race 267 and its persistence in a strain ($T \times 267$) established by mating a sister of the "first" hermaphrodite with a male (no. A112) Tippler.

purely genetic grounds, and they strongly suggest a maternal influence. Such an influence would be present if these *T* × *267* females produce unusual amounts of estrogen and pass it into their eggs, and if it there affects some of the male offspring as did injected estrogen in the experiments of Riddle and Dunham. Again, if these females actually produce unusually large amounts of estrogen while yolks and eggs are forming, this production is doubtless controlled by a genetic factor; the available data do not clearly determine that this factor is recessive.

If, however, estrogen alone were involved in the above results, we should expect that the sons of *T* × *267* females would be of comparable classes and frequencies regardless of the race to which the fathers belong. Actually, the evidence indicates that more extensive feminization occurs when the fathers are of *T* × *267* type than when they are of other types (such as *R* × *HC*). It is therefore suggested that race *T* × *267* carries a genetic factor which favors feminization, perhaps by lowering the threshold of estrogenic action on the embryonic testes. Whether this factor is likely to be the same as that responsible for the presumed hypersecretion of estrogen in the female is still a matter of pure conjecture. It is possible that several factors are involved; it is quite probable that the abnormally small testis size of race *267*, and the somewhat irregular testes of Tipplers (see below), were associated with factors which are present and active in the feminization of testes in race *T* × *267*.

The endocrine factor which is of special significance in the present study is best considered in connection with embryological data which show that a temporary hermaphroditic condition is "normally" present in the genetic male embryos of many species of birds and reptiles. Specifically, ovarian cortical tissue is present on the testes (particularly on the left testis) of doves[11] and pigeons[13] during the last few days of embryonic life. The atrophy of that ovarian tissue is complete at or slightly after hatching in ordinary races of doves and pigeons; this occurs, however, definitely later[13] in race *T* × *267*. Various investigators have shown that the injection of estrogen into the eggs of birds during early stages of incubation produces an increase in the amount of ovarian cortex on the testes and makes it persist longer, or even permanently. Riddle and Dunham showed that this effect could be obtained from estrogen injected into the muscles of the mother (ring dove), the time of this injection being so chosen that the mother's circulation would carry maximal amounts of estrogen to, and deposit it in, an ovum (yolk) which would ovulate 26 to 34 hours later. On the basis of their own results, and the related studies of others, Riddle and Dunham further concluded that "it is probable that much or all of the evanescent ovarian cortex normally found on the embryonic testes of birds and reptiles arises not through genic action but through action of estrogen."

Attention should next be directed to the data which show that, even in those males of the *T* × *267* strain which do not become true hermaphrodites, the ovarian cortex of the left testis disappears later than in the normal males of other strains[13] (fig. 163). This fact is made evident by the curves showing the percentages of males of the two types which retained some ovarian cortex at days 17, 18, and 23. At these ages the ovarian cortex, though absent in males of other races, was present in a very high proportion of males of race *T* × *267*. Moreover, since only a much lower proportion of the *T* × *267* males retain this ovarian tissue permanently (true hermaphrodites), some of the males which were utilized in these tests, and which showed ovarian tissue at 18 and 23 days, would doubtless have lost this ovarian tissue within a few days or weeks; on the other hand, it seems obvious that those few specimens which show this ovarian tissue in adult life (true hermaphrodites) have retained it from its first appearance in embryonic life. According to the study of Riddle and Dunham, an excess of estrogen by itself could apparently have produced in "normal races" a persistence of ovarian cortex equal to, or greater than, that actually found in race *T* × *267*.

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[13] Lahr, E. L., and O. Riddle, Anat. Rec., 1945, vol. 92, p. 425.

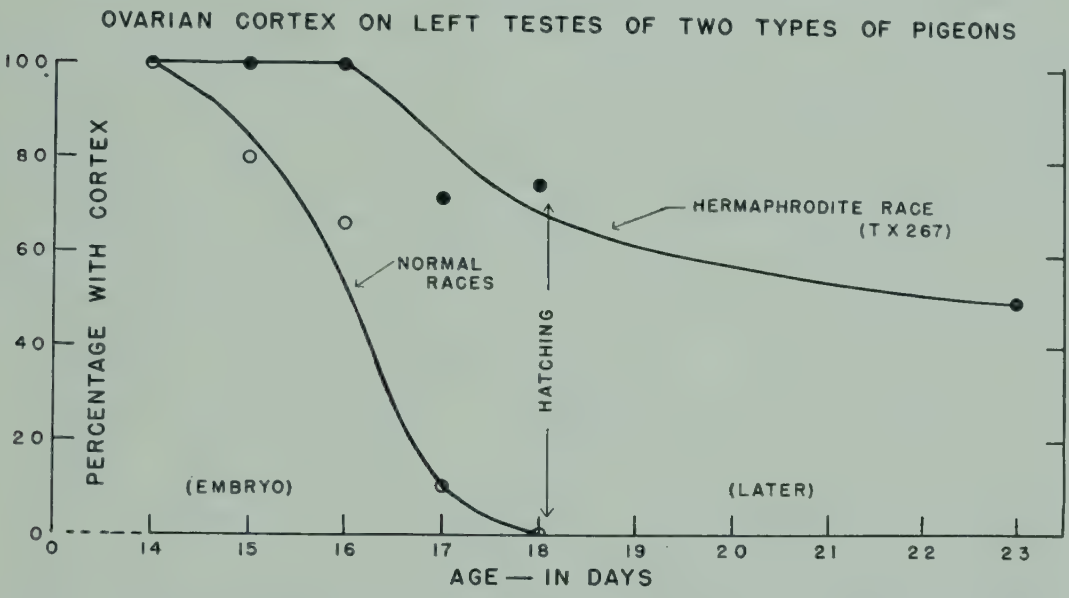

Fig. 163. Showing that before hatching, ovarian tissue tends to disappear on the left testes of normal races of pigeons, but to persist for a longer period in males of the hermaphrodite-producing race.

Comparisons of Measurements Made on This and Other Races

Data given elsewhere in this volume are utilized in making nearly all of the following comparisons. Data for the "F_+" generations of this hybrid material, when they are available, are here taken to represent "race" *T* × *267*.

The body weight of this race was intermediate to that of the parental races. Female body weights averaged 6 to 8 per cent less than that of males (including pseudohermaphrodites). Relative weight of the heart in race *T* × *267* is not remarkable, and the value found seems intermediate to the values obtained for the two parental races. Plumage weight was not measured in this race nor in race *267;* in Tipplers, however, plumage constituted a higher percentage of the body weight than was observed in any other breed of pigeons. Thyroid weights, though small, were definitely greater in *T* × *267* than in either parental race; this, however, may have resulted from the fact that a very high proportion of *T* × *267* offspring were bred under more goitrogenic conditions (after 1930). Observations not recorded in this volume showed[14] that, of the 7 pigeon types examined, the blood of race *267* had the highest hemoglobin content and erythrocyte count. In Tipplers these values were lower than the average values obtained for the 7 races. Less numerous measurements made on *T* × *267* indicated values for hemoglobin and cell count which were very close to the average obtained from the other 6 pigeon breeds. The basal heat production, and also the heat production at 20° C., of *T* × *267* (both sexes) was almost or quite indistinguishable from that of Tippler pigeons. The basal metabolic rate of males of these 2 races (and possibly of race *267*), however, when calculated in terms of surface area, was lower than that observed in any of 12 additional breeds or types.

Liver weight was not extreme, but relative to body weight it was markedly greater in race *T* × *267* (males, 2.09 or 2.34 per cent of body weight; females, 2.25 or 2.57 per cent) than in either Tipplers (males, 1.68 or 1.93; females, 2.04 or 2.32 per cent) or race *267* (males, 1.52 or 1.69; females, 1.50 or 1.68 per cent). The alternative figures given above are values obtained from birds with ascariasis. Similarly, intestinal length was relatively somewhat greater in this race (males, 2.66 or 2.76; females, 2.99 or 2.92 per cent) than in either Tipplers (males, 2.64 or 2.49; females, 2.75 or 2.70 per cent) or race *267* (males, 2.54 or 2.52; females, 2.79 or 2.87 per cent). Degree of responsiveness to prolactin was measured in only 6 races, but Tipplers and race *T* × *267* were far less responsive to this hormone than the other 4 races.

It is not known whether, or in what way, the three above-named items of evidence fit together; nor is it known whether they actually are related in any way to the hermaphroditism present in race *T* × *267*. Elsewhere (chapter 6) it has been noted that in pigeons prolactin has special ability to increase liver weight and to lengthen the intestine. Both these increases occurred in race *T* × *267*, and if these changes were mediated by prolactin they may have resulted either from an increased secretion of prolactin (to compensate for the very low sensitivity of the crop sacs?) or from a lowering in liver and intestine of the threshold of responsiveness to prolactin. Such a lowered threshold in the intestine, however, would seem rather paradoxical in a race whose crop sacs were known to give a minimal response to that hormone. On the other hand, if increased production of prolactin caused the increases in liver and intestine, that increase in prolactin would probably also be a factor in halting testis weight at the inferior level which, as noted above, also characterized this race.

Race *267* was especially remarkable in having testes whose median weight in relation to body weight was extremely small (0.38 per cent). Testis weight in race *T* × *267* was less extreme (0.48 per cent) but definitely inferior to that found in any other type except *267*. This value was rather low in Tipplers (0.59 per cent). The observed deficiency in testis size, in individuals of both hermaphrodite and normal types, could result from an increase of either prolactin or estrogen in the circulating blood.[15] Females of the two parent races produced their first egg in life at a median age of 6.7 months (Tipplers) or 8.1 months (race *267*). It is therefore somewhat surprising to find that the median age at maturity in females of race *T* × *267* is 8.9 months. Average weight of anterior pituitary glands was smaller in *T* × *267* than in most other races. Thus in race *T* × *267* (but not in F_1 and F_2 generations) age of females at sexual maturity was greater than in nearly all other races, testis size in males was smaller than in all other races except *267*, and size of anterior pituitaries was relatively smaller than in most other races. This group of facts might suggest that the output of gonadotrophin from the pituitaries of these birds is less than that in most other races. Possibly that is the case. On the other hand, if an excess of prolactin is put out by the pituitaries of these birds, the above facts would permit the view that simultaneous output of gonadotrophin may also be in excess of normal; excess of both prolactin and gonadotrophin would be consonant with greater liver weight, greater length of intestine, reduced testis size, and delayed age at sexual maturity —and perhaps with the production of increased amounts of estrogen, or with the change in tissue thresholds, which seems to constitute a factor for feminizing the reproductive organs of males.

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[14] Riddle, O., and P. F. Braucher, Amer. Jour. Physiol., 1934, vol. 108, p. 554.

Indirect Tests for Endogenous Estrogen Production in Males of This Race

It was not practicable to measure directly the estrogen in the blood of these birds, but indirect measurement was attempted. Plasma fat is known to increase greatly following all temporary increases in estrogen production in female pigeons and also following the injection of estrogens into pigeons of any age or sex;[16] and this action of estrogen seems to be highly specific. The rapid but rather inaccurate method of Allen,[17] which does not include phospholipids in the "fat" recovered, was used in these tests. During the summer and autumn of 1940, 1 to 8 measurements of the nonfasting plasma fat were made on most of the males (young and adult) of race *T* × *267* then alive. Some of these birds were killed within a few weeks, but others were sacrificed at 1 to 4 years after these measurements were made. When all autopsy data were available, these males were classified and the value of plasma fat for each class was calculated.

In 25 males which had no oviducts, the average value for plasma fat was 442 ± 13.6 mg. per cent; in 36 (of 37) males with oviducts (but not true hermaphrodites), the average was practically the same, 458 ± 13.6 mg. per cent. The additional (37th) male, whose oviduct weighed only 31 mg. when the bird was killed 6 months later (at the age of 69 months), gave the following six values, in milligrams per cent, during a period of 3 months: 560 (July 11), 656 (July 14), 928 (September 6), 2160 (October 11), 1760 (October 14), and 544 (October 16). In this case it seems certain, in the first place, that at some periods this male produced large amounts of estrogenic hormone, though at other periods (as proved by amount of plasma fat) this was nearly or quite the same as in other males; in the second place, the weight of the oviduct obtained at the time of killing (31 mg.) almost certainly indicates that exceedingly little estrogen was being secreted at that particular time; also, the amount of estrogen necessary to raise the plasma fat to 1700 and 2100 mg. per cent would almost certainly (on the basis of much additional experience) have caused a temporary increase of 10- to 50-fold (to 300 to 1500 mg.) in the oviduct of this bird. In other words, this case indicates that estrogen production in male pseudohermaphrodites fluctuates widely from one month, week, or year to another, and that single determinations of either plasma fat or oviducal weights provide information that applies only to a very restricted period of the life cycle. In true hermaphrodites, however, repeated laparotomies provided evidence that the oviduct was moderately sustained at all times.

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[15] Lahr, E. L., and O. Riddle, Endocrinology, 1944, vol. 35, p. 261.

[16] Riddle, O., T. Senum, and V. M. Rauch, pt. V *in* Riddle, O., and associates, Studies on carbohydrate and fat metabolism (Carnegie Inst. Wash. Pub. 569, 1947).

[17] Allen, N. N., Minnesota Agric. Exper. Sta. Bull. 130, 1938.

The above account may be completed by recording the small amount of data obtained on 4 birds which were either true hermaphrodites or males with highly aberrant testes. Two of these birds were quite immature when the samples for blood fat were taken, and only a single measurement was made on each bird. The values found for these 4 birds (240, 368, 384, and 512 mg. per cent) tend to be less, rather than more, than the averages obtained for other males of this race.

Considerable interest attaches to the general observation that many or most of the adult true hermaphrodites, and at least some of the pseudohermaphrodites, showed the wide separation of the pubic bones characteristic of laying females. This condition is generally thought to represent a response of these bones to estrogen.

Conclusions and Summary

A case of hermaphroditismus verus occurred in race 267. A normal sister of this hermaphrodite, when mated to a Tippler male, produced hermaphrodites in F_1 and later generations. Progeny in this strain consists of normal females, normal males, males with oviducts developed to various degrees (pseudohermaphrodites), and a few true hermaphrodites; the latter usually have a left ovotestis and a right testis and a fairly well developed left oviduct.

Both types of hermaphrodites are modified genetic males.

When outcrossed, the affected males do not seem to transmit the condition in F_1; but outcrossed $T \times 267$ females produce a high proportion of pseudohermaphrodites in F_1. These results are difficult to account for on a purely genetic basis, and they strongly indicate a maternal (nongenic) influence. It is suggested that this influence is exerted through unusual quantities of estrogen produced by mothers and accumulated in some or many of their ovarian eggs; during embryonic development this estrogen magnifies and perpetuates the formation of ovarian cortical tissue on testes (no effect on ovaries) in the way earlier observed by Riddle and Dunham. This ability of females of a race to produce unusual amounts of estrogen during egg production would apparently rest on the presence of a recessive genetic factor.

Since the data indicate that more extensive feminization of sons occurs when *T* × *267* females are mated to males of their own breed, it is suggested that race *T* × *267* carries a genetic factor which favors feminization, perhaps by lowering the threshold of estrogenic action on the embryonic testis. It is not known whether this factor is the same as that responsible for the presumed hypersecretion of estrogen in females at reproduction.

Although a first case of true hermaphroditism arose in race *267*, it is believed that Tipplers, more specifically Tippler male no. A112, contributed to the genetic background of the hermaphroditism exhibited in race *T* × *267*.

Various characteristics of Tipplers and of race *267* which might be associated with ability to transmit hermaphroditism are reviewed. Diminutive testes in race *267*, irregularly shaped testes in Tipplers, and undersized testes in race *T* × *267* seem to be involved in this type of hermaphroditism; females of race *T* × *267* tend to mature later than do females of either parent race. These two items suggest a reduced (or delayed?) production of gonadotrophin by the pituitaries of *T* × *267* individuals. Relatively greater liver weight and intestinal length than in parent races suggests, however, an increased production of prolactin in race *T* × *267*. If this is the case, the amount of gonadotrophin produced by these birds could perhaps be normal or in excess of normal.

Limited numbers of measurements were made on the plasma fat of various types of *T* × *267* males (including hermaphrodites) in an effort to obtain an indirect measure of estrogen production in these types of males. Differences between types were not obtained. Data from one pseudohermaphrodite showed, however, that it produced much estrogen at certain periods and little or none at other periods; these data further showed that the size of the oviduct, as observed at autopsy, provides information concerning current production or lack of production of estrogen, but gives little or no indication of the much larger size which it may have attained at earlier periods.

Adult hermaphrodites commonly showed the wide separation of pubic bones which normally occurs in reproducing females as a result of estrogen production.

Relatively large left oviducts (up to 1.9 gm.) were obtained in so-called pseudohermaphrodites whose two testes were without tissue which could be identified histologically as ovarian. The presence of oviducts of this type in such birds indicates the production of large amounts of estrogenic hormone; and thus, on the basis of their internal secretions, even the gonads of these birds are partly female and bisexual.

11

DATA ON WEIGHT OF HEART, SKELETON, AND PLUMAGE IN CERTAIN RACES AND HYBRIDS OF DOVES AND PIGEONS

This chapter presents data on three topics which are of rather special interest in connection with the measurements of heat production described in part II of this volume. To some extent these somewhat heterogeneous materials also supplement the studies on constitutional differences described in previous chapters. None of the organs or systems which are to be considered here were studied in all races. Indeed, the data for weight of the dry skeleton and for weight of the plumage seem almost fragmentary; it was thought essential, however, to learn whether differences in these two nonmetabolizing kinds of tissue can account for observed effects of age, sex, and race in basal heat production. On *a priori* grounds it was considered probable that heart weight would be more closely correlated with heat production than with previously considered constitutional elements. The literature dealing with the relation of each of these three organs, or organ systems, to heat production is considered elsewhere (part II).

Heart Weight

The data on heart weights were obtained from birds considered healthy, and included in this group were birds lightly parasitized with roundworms (ascariasis). Nearly all the data were obtained from adults; approximately 5 per cent of the data were from younger birds, aged 4 to 6 months. All data were obtained between 1928 and 1945, the period during which measurements of heat production were made on these birds. The data are presented in the form of percentile analyses, and median heart weight is further calculated as percentage of body weight. It is to be noted that "body weight" was obtained on the intact bird; "heart weight," however, was obtained on the exsanguinated bird.

Figure 164 and additional data indicate that, in doves and pigeons of all races and both sexes, median heart weight varies between 0.9 and 1.3 per cent of the body weight. Coefficients of dispersion generally run around 0.09. Data for the 12 dove races which provided most measurements are given in figure 165. Lowest percentages of body weight were obtained in races *N1*, *63*, and *N2*; relatively largest hearts were obtained in races *51*, *72*, and *75*. In general, both the above groups of races had intermediate rather than extreme rates of heat production.

Data for 18 types of dove hybrids are given in figure 166. Relatively lowest heart weights (medians) were from hybrids *63* × *N2*, *11* × *62*, and *63* × *62*; relatively heaviest hearts were found in hybrids *62* × *B*, *72* × *75*, and *72* × *N1*.

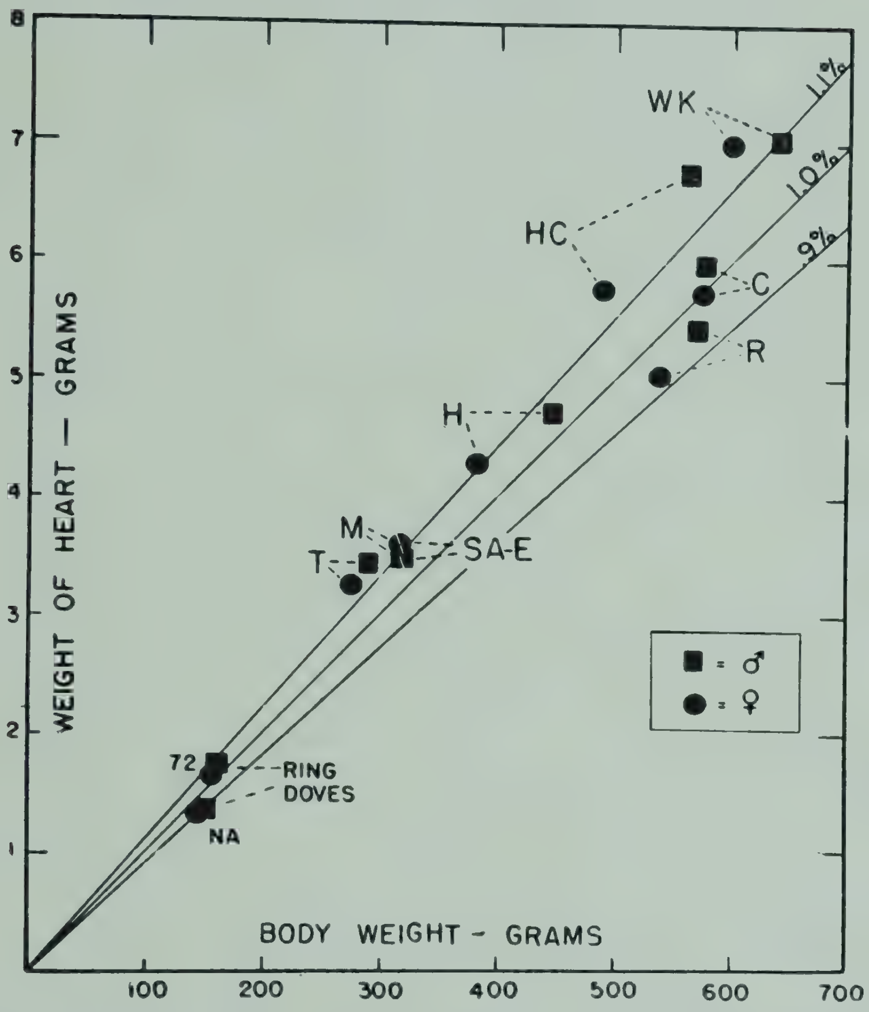

FIG. 164. Showing that relative weight of the heart is approximately the same in doves and in pigeons, and in the two sexes of both species.

These hybrids, like the pure races noted above, usually had intermediate rather than extreme rates of heat production.

Heart weights from several of the smaller races and hybrids of pigeons are analyzed in figure 167. Relatively lowest median values were obtained from *SA-E* × *267* hybrids, from *SA-R* scragglies, and from *T* × *SA-E* hybrids. Highest values were from race *T*, and from hybrids *T* × *H* and *M* × *299*. In these cases heart weight shows no clear association with rate of heat production.

Data from the larger pigeon races and hybrids are analyzed in figure 168. Relatively smallest hearts were from Runts (*R*), *R* × *M*, and *R* × *SA-E* hybrids. All these types had low or extremely low rates of heat production. Relatively heaviest hearts were obtained from *R* × *HC* hybrids, from Homers *C*, and from *T* × *R* hybrids. Heat production was adequately studied only in the *R* × *HC* hybrids; their rate of heat production was extremely low. At the bottom of this graph are data from young (2.0 to 3.0 months) Carneaux. It will be noted that relatively and absolutely heavier hearts were obtained from these young than

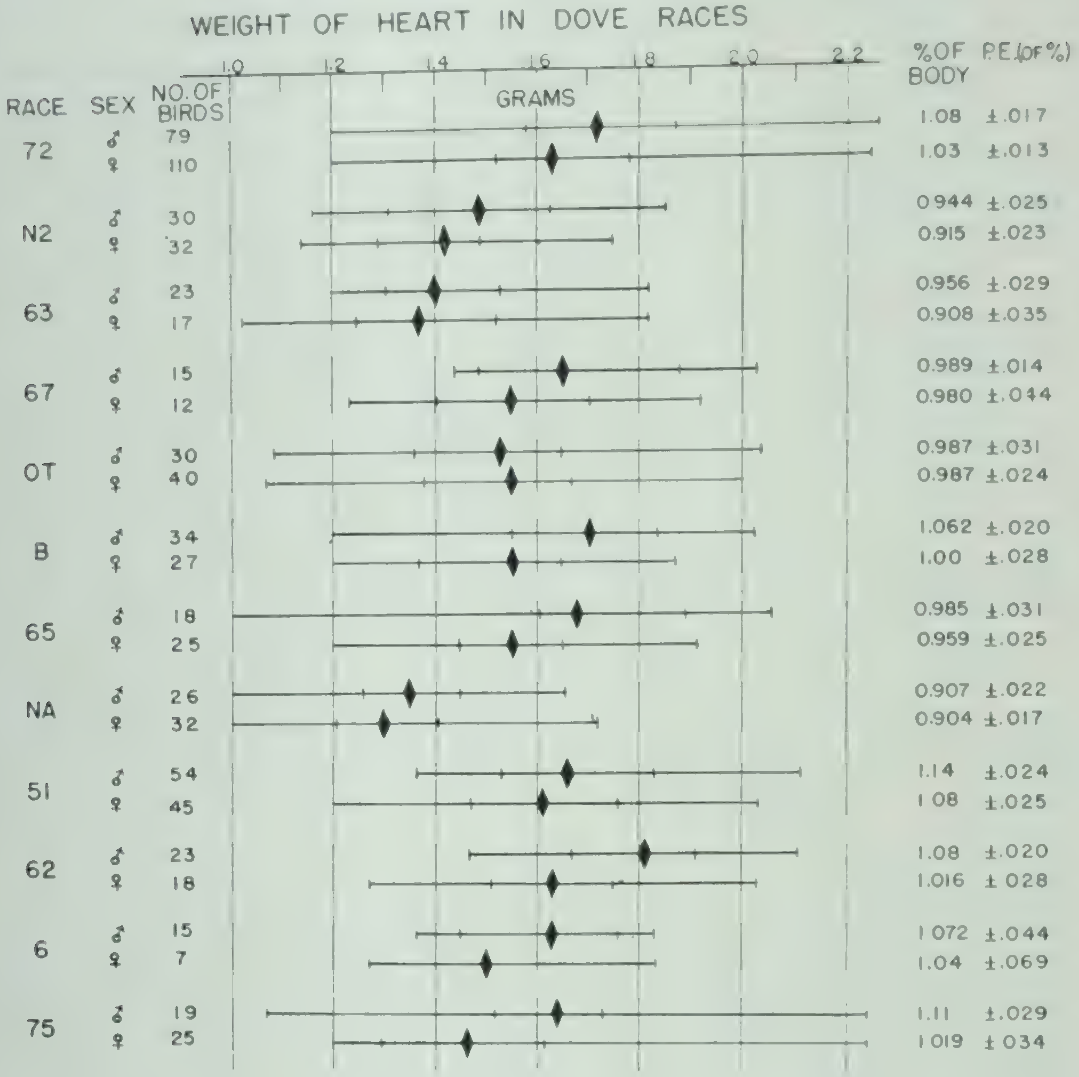

FIG. 165. Percentile analyses of the heart weights of the two sexes of 12 races of doves

from the adult Carneaux (*C*) listed in the upper part of the graph. Studies conducted on some of these Carneaux showed a higher rate of heat production in the young than in the adults.

The data presented in figures 165 to 168 supply information on the question of a sex difference in relative heart weight. Very few cases of statistically significant sex difference were obtained. Significance, or near significance, is observable, however, in the cases of dove races *72*, *62*, *75*, and *51*, and hybrids *72* × *OT*, also pigeon types *R* × *HC*, *SA-R* normal, and *267*. Moreover, a marked predominance of slightly larger percentages in males (groups) of the various types of doves is notable. Thus, in 11 of the 12 races the value for the males is slightly larger, and in the twelfth case the values are equal; in 12 of the 18 types of dove hybrids the male hearts are larger, in 4 they are smaller, and in 2 there is equality. In pigeon types, however, there is a slight predominance of cases in which relative size of the heart is at least somewhat greater in the female. The mean, and

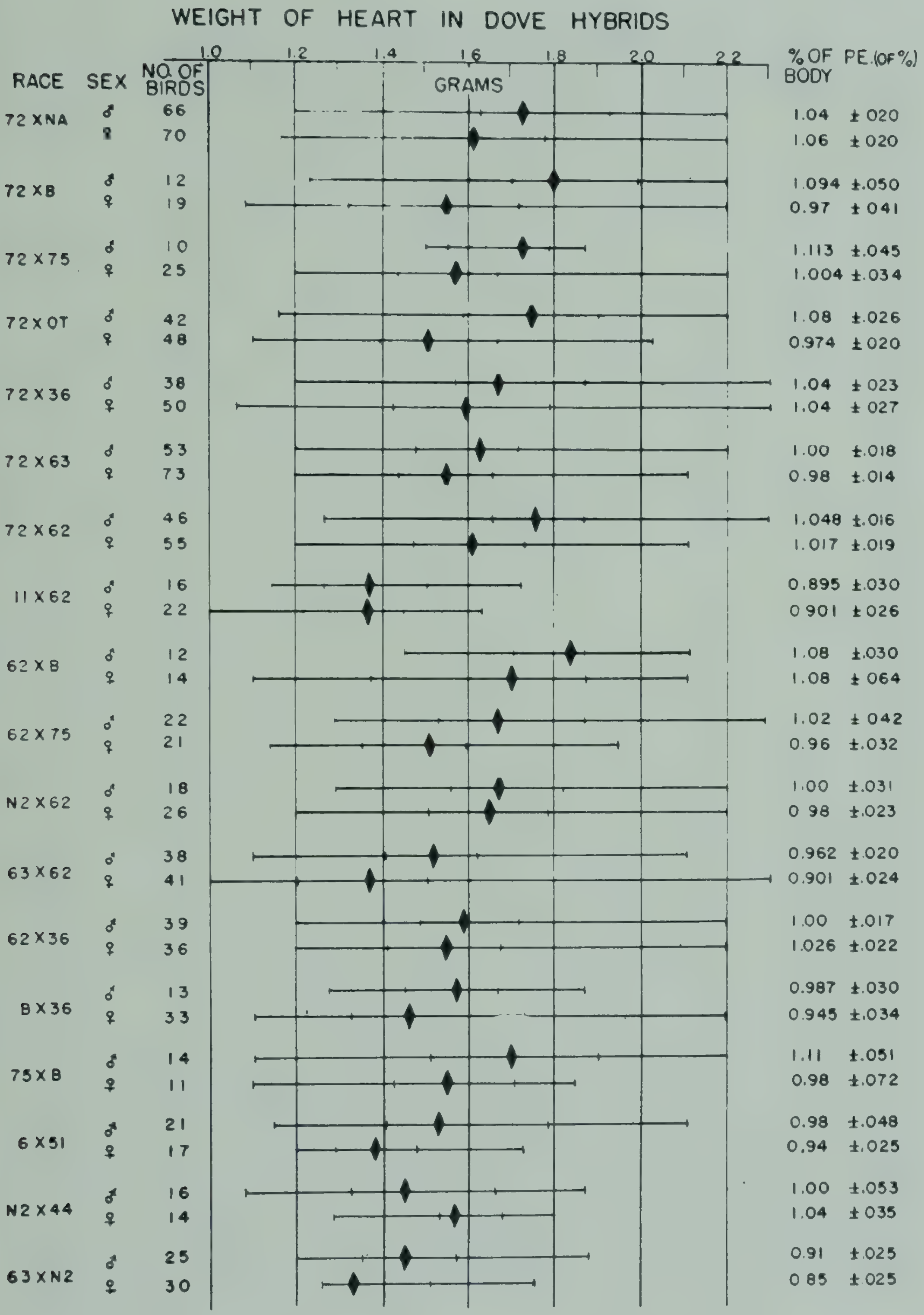

FIG. 166. Percentile analyses of the heart weights of the two sexes of 18 types of dove hybrids.

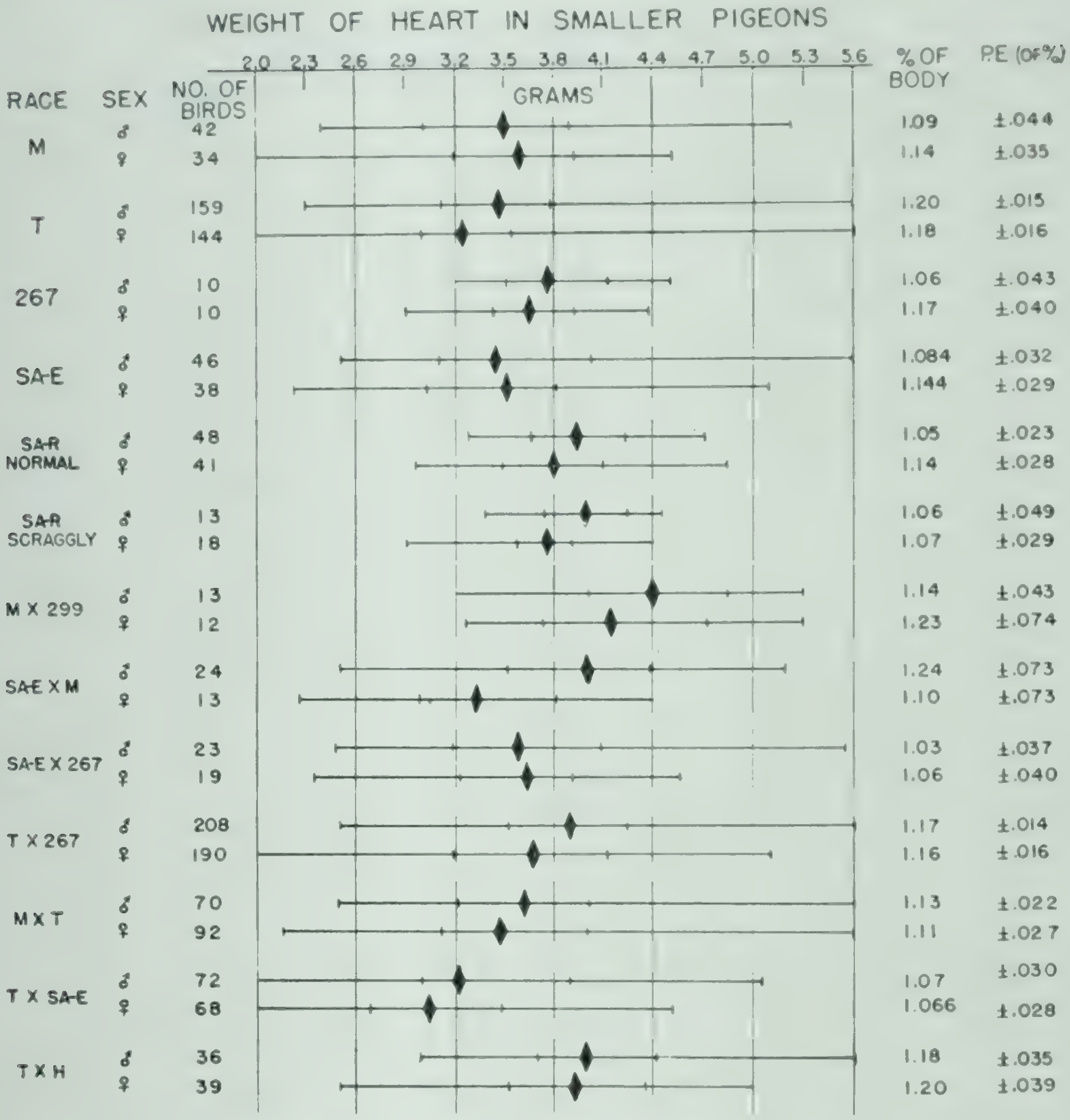

FIG. 167. Percentile analyses of the heart weights of the two sexes of 13 smaller types of pigeons.

the standard error, of the values obtained from males of the 30 types of doves is 1.022 ± 0.012 per cent; for females, 0.983 ± 0.010 per cent. The mean of values for 25 types of adult male pigeons is 1.101 ± 0.018 per cent; for females, 1.110 ± 0.014 per cent.

DRY WEIGHT OF SKELETON

The adults used in this study were aged 5.8 to 48 months; the young, 2.6 to 3.6 months. Skeletons were carefully cleaned and weighed, and most of the remaining organic substance was separated from them in slowly boiling alkaline solution; thereafter they were dried (7 to 10 days) at 96 to 98° C. The data obtained for the dry skeleton, in terms of percentage of body weight, are surveyed in figure 169. This graph indicates, as might be anticipated, that the dry skeleton repre-

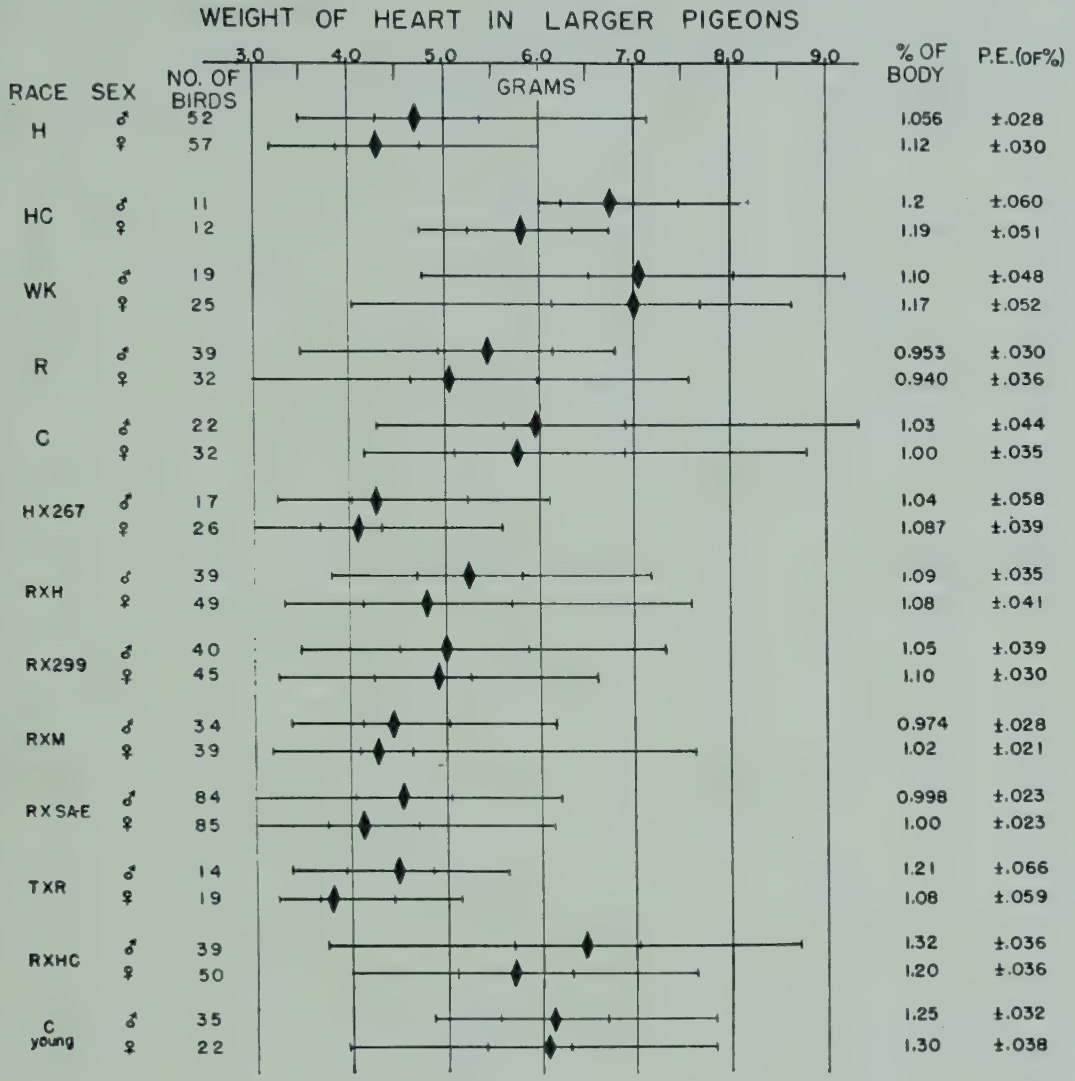

FIG. 168. Percentile analyses of the heart weights of the two sexes of 12 types of adult pigeons and 1 type of young pigeons.

sents higher percentages of the body weight in the (heavier) pigeons than in doves.

Data for both doves and pigeons are analyzed in figure 170. The skeletons of young birds tend to have smaller median percentages of dry matter (and more water) than is found in skeletons of adults of corresponding type. The difference is small, however, and the values are highly variable in both age groups. Coefficients of dispersion are rather small, usually near 0.05. Significant racial differences among doves may exist, but they were not established by the small amount of data available. Values obtained for the several pure races of doves are therefore grouped together; likewise all data obtained from dove hybrids are thrown into a single group. The percentage dry weight of the adult skeleton does not appear to be significantly different in pure races from that in hybrids (median value for both, 3.42 per cent). Again, in the young there is no evidence of sex difference in

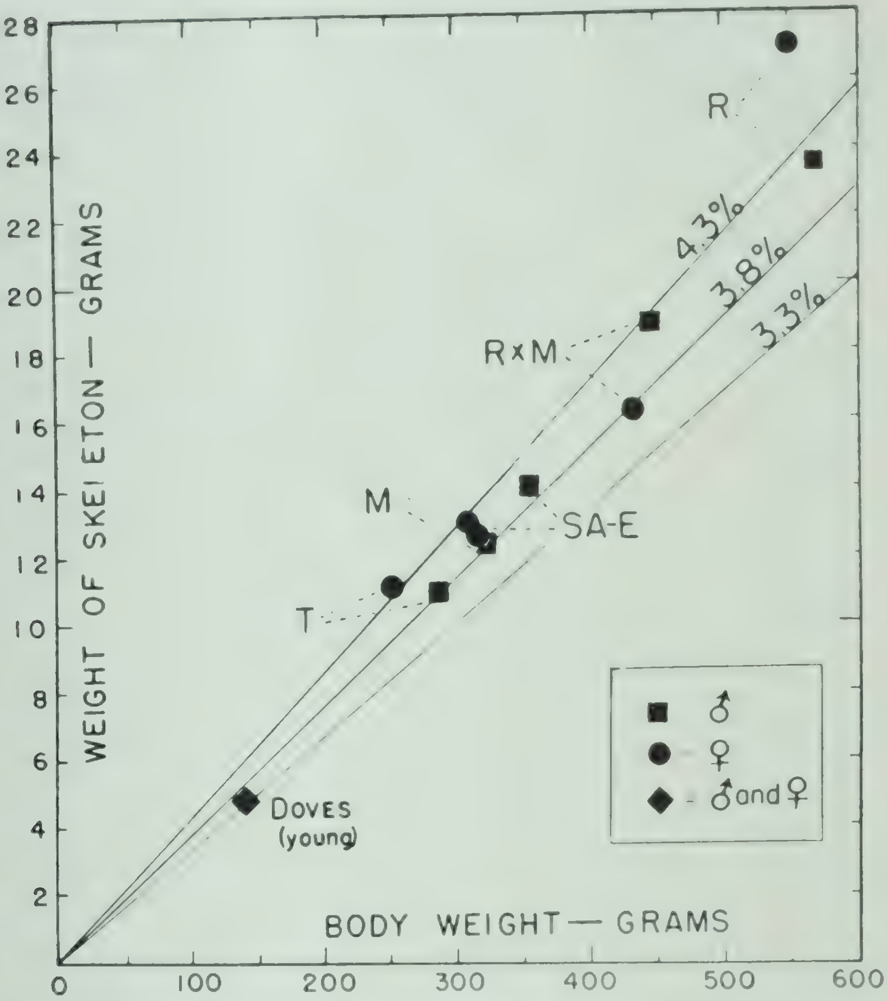

Fig. 169. Survey of data for weight of the dry skeleton in the two sexes of 4 types of pigeons.

skeletal weight. In adult doves a significant sex difference seems to exist, but to rest solely on the fact that a few females sometimes show unusually heavy bones. Our breeding data have been closely examined with a view to learning whether these heavy bones were found only in females temporarily provided with medullary bone formed during (and persisting for 10 to 20 days after) heavy production of estrogen.[1] This examination of data obtained from both doves and pigeons provided no clear answer. The solution of this question is further complicated by the fact that young males showed greater variability than did either adult males or young females. Median values obtained for adult doves indicate that the dry weight of the female skeleton exceeds that of the male by less than 0.1 per cent of the body weight. Sex differences in inert or nonmetabolizing skeletal tissue are therefore not responsible for any observed differences in heat production.

The racial differences observed in dry (also in moist) skeletal weights of pigeons are in accord with the body weights of the various breeds; thus, for a few adults

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[1] Riddle, O., V. M. Rauch, and G. C. Smith, Anat. Rec., 1944, vol. 90, p. 41.

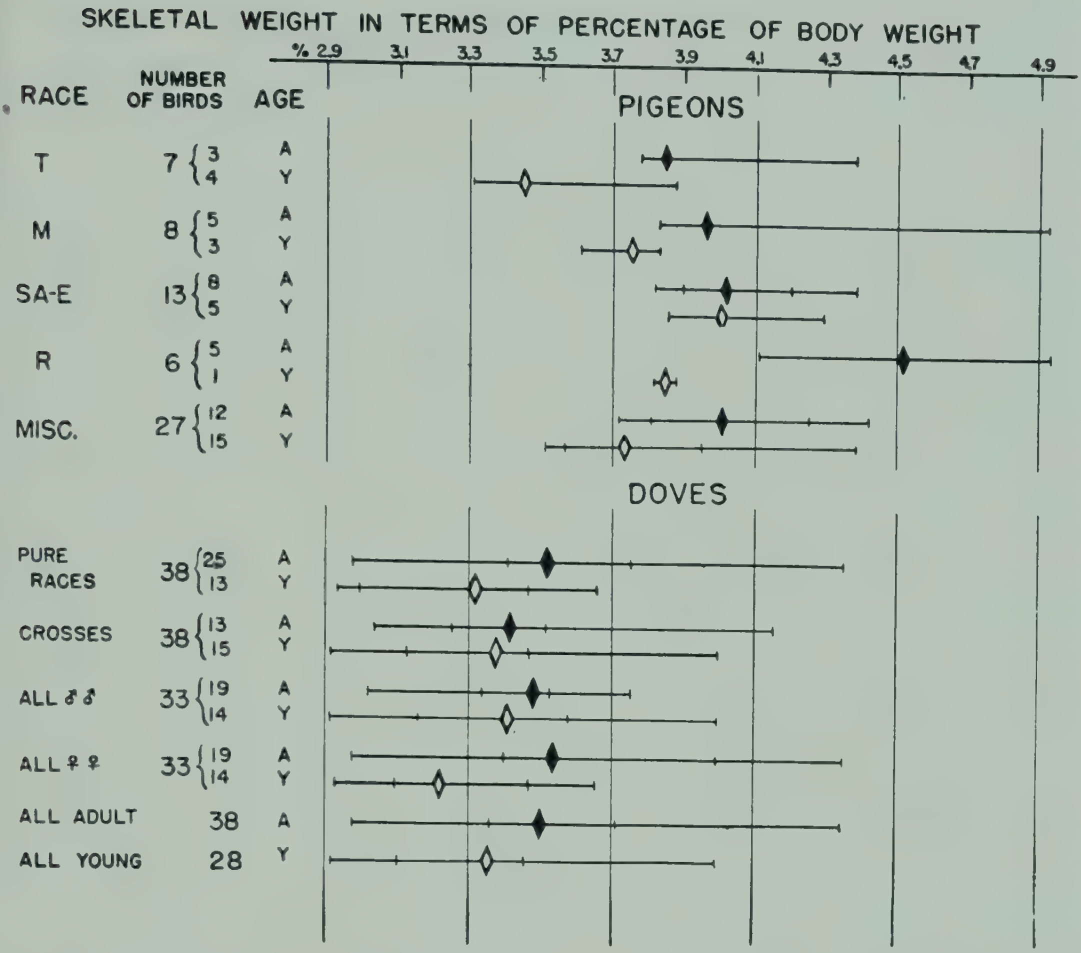

Fig. 170. Percentile analyses of data for weight of the dry skeleton in certain types of pigeons and doves. The differences are related to body weight. A = adult; Y = young.

of the smallest race (Tipplers) a median value of 3.85 per cent, and for the largest race (Runts) a value of 4.52 per cent, was obtained. The above data are in good accord with Weiske's[2] findings on fowl. For example, in a chick of 405 gm. Weiske reported that the dry skeleton represented 4.0 per cent of the body weight; in an adult of 1360 gm. this value was 6.0 per cent.

Moist weight of the skeleton, in terms of percentage of body weight, was not significantly different in young and adult birds nor in the two sexes. For selected and comparable pigeons belonging to races of small or medium size, and eliminating one adult female with abnormally high skeletal weight, the percentages for the various groups were as follows: adult males, 6.69; adult females, 6.72; young males, 6.61; young females, 6.76. Comparable groups of ring dove males, adult and young, gave an average value of 6.22 per cent; all females of these same groups, old and young, gave an average of 6.30 per cent.

Average percentages of water found in the moist skeletons of the various classes were as follows: Dove males, adult, 43.2; young, 48.5. Dove females, adult, 42.8; young, 47.7. Pigeon males, adult, 40.6; young, 45.0. Pigeon females, adult, 39.3; young, 47.0. The water content of the skeletons of the doves and pigeons studied was therefore approximately 5 per cent greater in the young than in the adults.

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[2] Weiske, H., Landwirtschaftlichen Versuchsstationen, 1889, vol. 36, p. 81.

Weight of Plumage

The same birds which were used above to obtain weights of the skeleton, and several additional adults, were used in the present incomplete study of the weight of the plumage of doves and pigeons. Only some of the more important races were investigated. All the data were obtained between January 1 and August 23, and nearly all were obtained in 1928. In view of the relatively high variability of the values obtained, the number of individuals studied is too small to provide a satisfactory measure of the plumage weight of most of the races studied. Coefficients of dispersion vary around 0.06. Though the molting of feathers (or unequal stages of molt) affected the values obtained, it is not possible to attribute a major part of the observed variability to that cause. A part of this variability is associated with immaturity and maturity; another part, at least in some cases, is associ

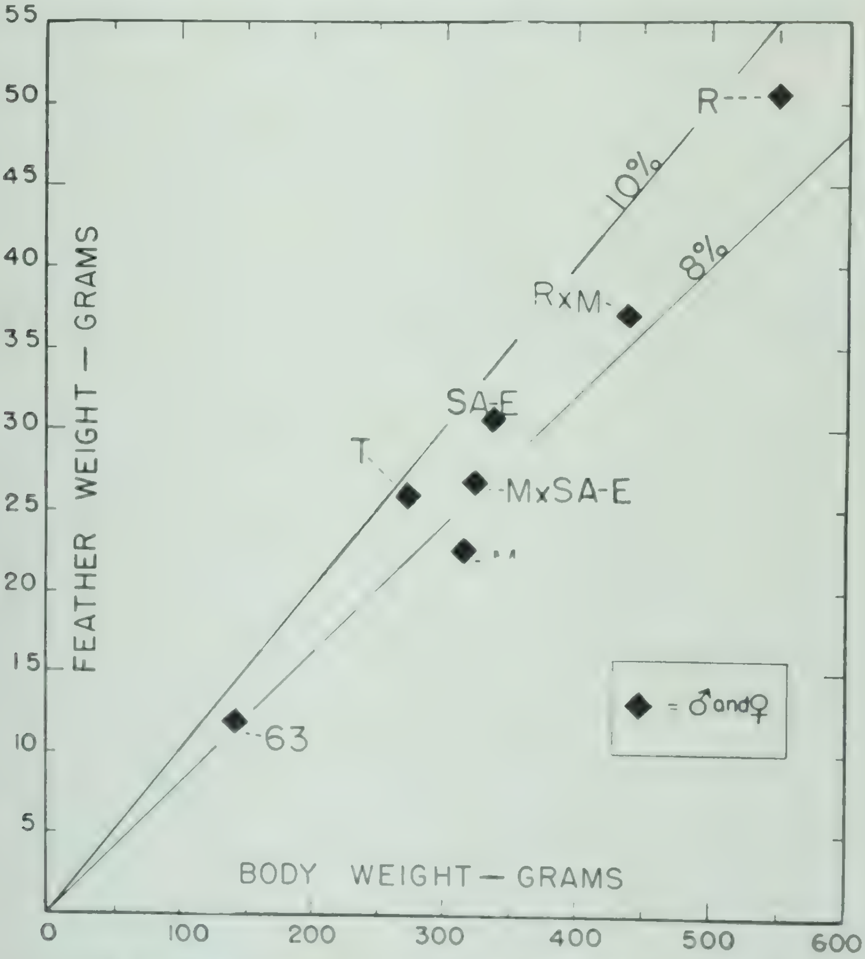

Fig. 171. Graph showing relative weight of the plumage in 6 types of adult pigeons (sexes combined) and in doves of race 63.

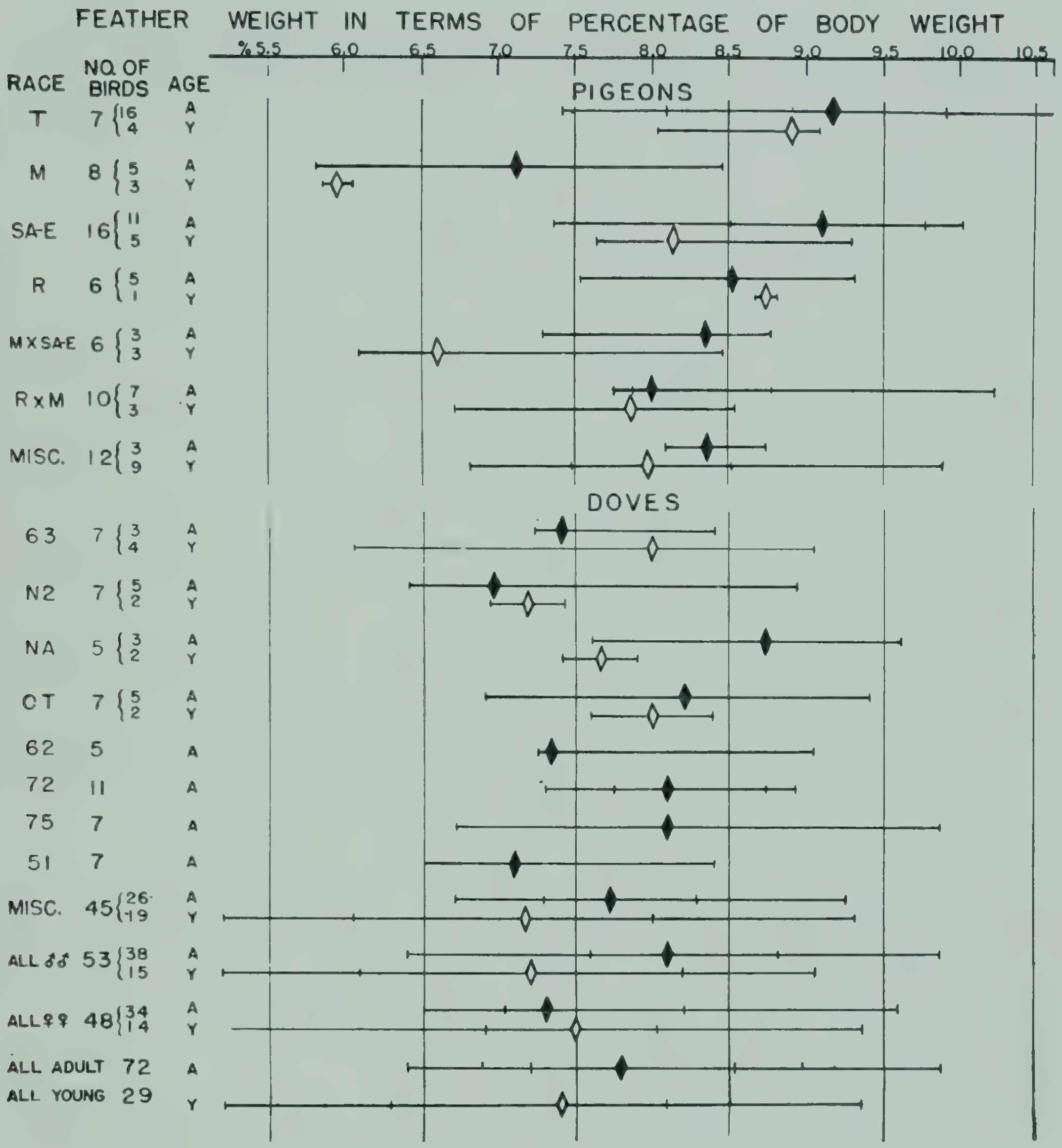

Fig. 172. Percentile analyses of data for plumage weight in pigeons and doves. Differences due to race and age (A = adult; Y = young) are shown. Sex difference in doves is indicated; for sex difference in pigeons, see text.

ated with race. A survey of results obtained for adults of certain types is given in figure 171.

A partial analysis (sexes not separated) of the data is given in figure 172. It should be stated at once that the percentile analyses which summarize data for the two sexes and for the two age groups of doves are unwarranted if racial differences exist among these doves. This follows from the fact that the various races and sexes are not equally represented in these summaries. If no racial differences are present, these summary statements seem useful.

The data make it apparent that, in terms of percentage of body weight, our stock of Magpies (*M*) have a lighter, and our Tipplers (*T*) a heavier, plumage than was found in most other breeds of pigeons. Also, in race *SA-E* plumage weight was apparently slightly greater than in most of the other breeds. Wriedt and Christie[3] noted that Magpies have very short feathers. The evidence suggests that plumage weight was less in races *N2* and *51* than in typical dove races. These two races and the Magpies all had unusually high rates of heat production.

Some additional data concerning age and sex difference in plumage weight are supplied in the following paragraphs. Examination of average values obtained for the two age groups indicates that in the present samples the actual plumage weight of the young doves was approximately 5 per cent less than that of the adults. Since the body weights of the two groups were practically equal, these young birds had about 5 per cent less "nonmetabolizing tissue" (plumage), and about 5 per cent less "insulating material," than was found in the adults.

Details of data for plumage weight, as percentage of body weight, provide the following information on sex difference. The adult males of all the 4 pigeon races had heavier plumage than adult females of their respective races. The mean value obtained for the 4 races was 9.06 per cent for males and 8.03 per cent for females. Thus the females of these races of pigeons apparently had 1.0 per cent less of this "nonmetabolizing tissue," and 11 per cent less total "insulating material," than did the males. The very inadequate data for hybrid pigeons suggest a smaller difference in the opposite direction. The limited data obtained from young pigeons, races and hybrids, provide no evidence of a sex difference. Nine of the 10 dove races or types in which birds of the two sexes were measured indicated higher relative plumage weights in the males. The mean value obtained for the 10 groups of males was 8.29 per cent; for females, 7.70 per cent. If these values are applicable to all types of doves, they indicate that females of this species have 0.6 per cent less "nonmetabolizing material" (plumage), and 7 per cent less total "insulating material," than do males.

Conclusions and Summary

In adult doves and pigeons, median heart weight was found to vary between 0.9 and 1.3 per cent of the body weight. In young pigeons of a single breed (Carneaux), heart size, in terms of percentage of body weight, was markedly greater in the young (1.275 per cent) than in adults (1.015 per cent).

For doves, relatively smallest heart weights were obtained in races *NA*, *63*, and *N2*, and in hybrids *63* × *N2*, *11* × *62*, and *63* × *62*. Relatively largest heart weights were obtained in races *51*, *72*, and *6*, and in hybrids *62* × *B*, *72* × *75*, and *72* × *NA*. Pigeon types with relatively lowest heart weights were Runts, and *R* × *M* and *R* × *SA-E* hybrids; those showing highest values were *R* × *HC* hybrids, Homers *C*, and *T* × *R* hybrids.

Extremes of heart weight (racial) in this material were rarely associated with extreme rates of heat production as this was measured in part II of this study. Hybrids *R* × *HC* constitute an exceptional, and quite unexpected, group which had relatively heavy hearts and a very low rate of heat production. Race *N2* was also exceptional, but here these relationships are reversed.

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[3] Wriedt, C., and W. Christie, Ztschr. f. indukt. Abstam.- u. Vererbungsl., 1926, vol. 42, p. 93.

Heart weight is relatively slightly higher in pigeons (1.101 ± 0.018 per cent in males, 1.110 ± 0.014 per cent in females) than in the (smaller) ring doves.

Heart weight, in terms of percentage of body weight, is generally slightly greater in dove males (1.022 ± 0.012 per cent) than in females (0.983 ± 0.010 per cent). Most types of doves agreed with this general trend. In pigeons, however, the present data supply little evidence for the existence of a sex difference in (percentage) heart weight.

Weight of the fresh and dry skeleton was obtained for a few types of young (2.6 to 3.6 months) and for small numbers of adult doves and pigeons of both sexes. The water content of the skeletons was approximately 5 per cent greater in young than in adults (young 48.1 per cent, adults 43.0 per cent in doves; 46.0 and 40.0 per cent respectively in pigeons). The dry skeletons of young birds were approximately 5 per cent lighter than those of adults.

The moist weight of the skeleton in doves, of both age groups and of both sexes, was approximately 6.3 per cent of the body weight. In pigeons of small or medium body weight this value was approximately 6.7 per cent.

Racial differences in weight of the skeleton of breeds of the same body weight were not demonstrated in the present material. The relative weight of the dry (also the moist) skeleton of the various breeds increases with increase of body weight; thus, in order of increasing body size, median percentages of 3.42 (doves), 3.85 (Tipplers), and 4.52 (Runts) were obtained.

A slight sex difference in skeletal weight was observed in adults only, and there the difference rests on the fact that a few females have (temporarily or permanently) unusually heavy bones. The median value for adult female skeletons exceeded that for males by less than 0.1 per cent of the body weight in doves and by 0.3 per cent in pigeons; this difference in amount of inert or "nonmetabolizing" tissue would not measurably affect rates of heat production in the two sexes.

Plumage weight was obtained for a few young and adult individuals of some typical races of doves and pigeons. The data are presented in terms of percentage of body weight.

Besides the variability incident to unequal stages of molting, other variability was observed. Average plumage weight of young birds (aged 2.0 to 3.0 months) was approximately 0.5 per cent (doves) or 1.0 per cent (pigeons) lighter than that of corresponding adults. Thus young doves have about 0.5 per cent (pigeons about 1.0 per cent) less "nonmetabolizing plumage tissue," and about 5 per cent (pigeons about 11 per cent) less total "insulating material" than was found in the adults.

Magpies apparently have significantly lighter, and Tipplers and *SA-E* significantly heavier, plumage than was found in some other breeds of pigeons. Racial differences among doves were not demonstrated by the available data, but values obtained for races *N2* and *51* were lower than those obtained for other races or types.

Data for sex difference in relative plumage weight in the four available races of pigeons indicate heavier plumage in males (9.06 per cent) than in females (8.03 per cent). Thus the body weights of these females seem to include 1.0 per cent less of this "nonmetabolizing tissue" and 11 per cent less total "insulating material" than is found in males. A smaller amount of data from pigeon hybrids was not in agreement with this result.

Data for sex difference in relative plumage weight in 9 of 10 dove races or types indicated higher values in males (8.29 per cent) than in females (7.70 per cent). If these values apply to all dove types, they indicate that the body weights of these females contain 0.6 per cent less of this "nonmetabolizing tissue" and 7 per cent less total "insulating material" than is found in males.

In terms of percentage of body weight, the total of nonmetabolizing tissue (dry skeleton plus plumage) differs in various groups by the following amounts: young, 5.5 per cent (doves) or 6.0 per cent (pigeons) less than in adults; females, 0.5 per cent (doves) or 0.7 per cent (pigeons) less than in males.

Part II

12

GENERAL STATEMENT ON BASAL HEAT PRODUCTION

Problems

Conditions subsequently discussed make it evident that the role of *race* in heat production can perhaps be satisfactorily determined only in groups reared and kept under conditions which are nearly or quite identical in many respects. Again, if or when differences are found between races thus reared and maintained, it then becomes a matter of prime importance to have additional information concerning those constitutional factors—structural, functional, genetic—which are most directly related to the observed racial difference in metabolic level. The races of doves, and the races of pigeons, utilized in the present study should meet the requirement of exposure to practically identical conditions, and the special studies conducted upon them (part I) should contribute much to an interpretation of observed racial differences, at least in the case of certain races.

Since some of the dove races were selected on the basis of the weights of their thyroids, and since weight alone provides no measure of thyroid activity, the present measurements of heat production were relied upon to supply definite information on that point. It may be noted at once that no previous study has established this type of racial distinction in either animals or man; the present study has succeeded in establishing a number of such racial types. This successful effort, and available data[1] concerning genetic factors for susceptibility to goiter in man, make it probable that human populations (strains) characterized by higher or by lower rates of heat production, and by corresponding high or low thyroid activity, could be established in man.

The effect of *hybridity* on heat production is a matter of high biological interest on which practically no information is available. The present data contribute something, though not much, to this subject. Data of first importance could be obtained only on F_1 hybrids, and for none of the numerous types of hybrids included in this study was the available number of individuals sufficient to fix the status of such hybrids. In every case, therefore, data for later generations were combined with the data obtained from F_1. Such combined data clearly show that hybrids from our ring dove races tend to have a basal heat production intermediate to that of the parent races. This result can be said to provide an item of information concerning hybridity, and at the same time it seems to support the conclusion that the values obtained for the (parent) races are fairly accurate. Hybrids obtained from established breeds of pigeons yielded less uniform results. A few of them apparently tend to have rates of heat production higher than that of either of the parental races.

Many studies have been made on the role of *sex* in heat production. For man, and perhaps for one or two other species, present information is perhaps fairly satisfactory if we are concerned solely with results of measurements made under a single set of conditions—adopted for standard or basal measurements—and if the cause or source of the difference is left out of account. In addition, however, it is highly desirable to learn the extent to which sex affects the amount of change in rate of heat production when individuals make adjustments to different thermal environments. For this reason the present measurements have been made on birds subjected to three environmental temperatures: 30°, 20°, and 15° C. It was initially suspected, and later demonstrated,[2] that it may be unsound to regard the minimal values obtainable at thermal neutrality (30° C. in doves and pigeons) as an adequate measure of the metabolic status of a race or sex. Perhaps temperature, like some drugs, certain diseases, undernutrition, and prolonged inactivity, may drive oxygen consumption to an abnormally low value.

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[1] Cited in chapter 3.

The results obtained clearly show that *season* has marked influence on the heat production of doves and pigeons. Again, the possibility that *age* may affect metabolic rate, and the importance of evaluating this factor, have compelled a separate presentation of data obtained from older birds. Thus the data obtained for each race must be subdivided for the three temperatures used, for sex, for the four seasons, and for age. As a consequence of these (and other related) requirements the present data must be presented in tabular form.

METHODS

All measurements were made in the multiple-chamber apparatus of Benedict,[3] upon or around which the author constructed a cooling device (insulated glass box) which permitted the maintenance of the four chambers of the apparatus at any desired temperature (5° to 35° C.). Very cold calcium chloride brine was pumped, as needed, into tanks fitted into the tops of these insulated boxes. Two sets of the apparatus, allowing the simultaneous study of eight birds, were employed. Only four of the eight chambers were equipped with double sets of carbon dioxide absorbers, and thus respiratory quotients were obtained for only four of the eight birds. The two sets of apparatus are shown in plate 6.

The physiological technique employed to obtain reproducible values from these birds was the subject of two years of preliminary study. The results of that study, done in collaboration with Dr. F. G. Benedict, were published in full.[4] The chief items of that technique will be briefly redescribed here. Only mature birds (5+ months old) were used except in a few tests which are separately tabulated. The 8 birds selected on any day were chosen from a colony of approximately 1000 birds, of which about 600 were mated pairs. Birds which were brooding, or whose reproductive records failed to indicate good health, were not used; in some cases later autopsy showed certain birds to be diseased and led to the exclusion of data

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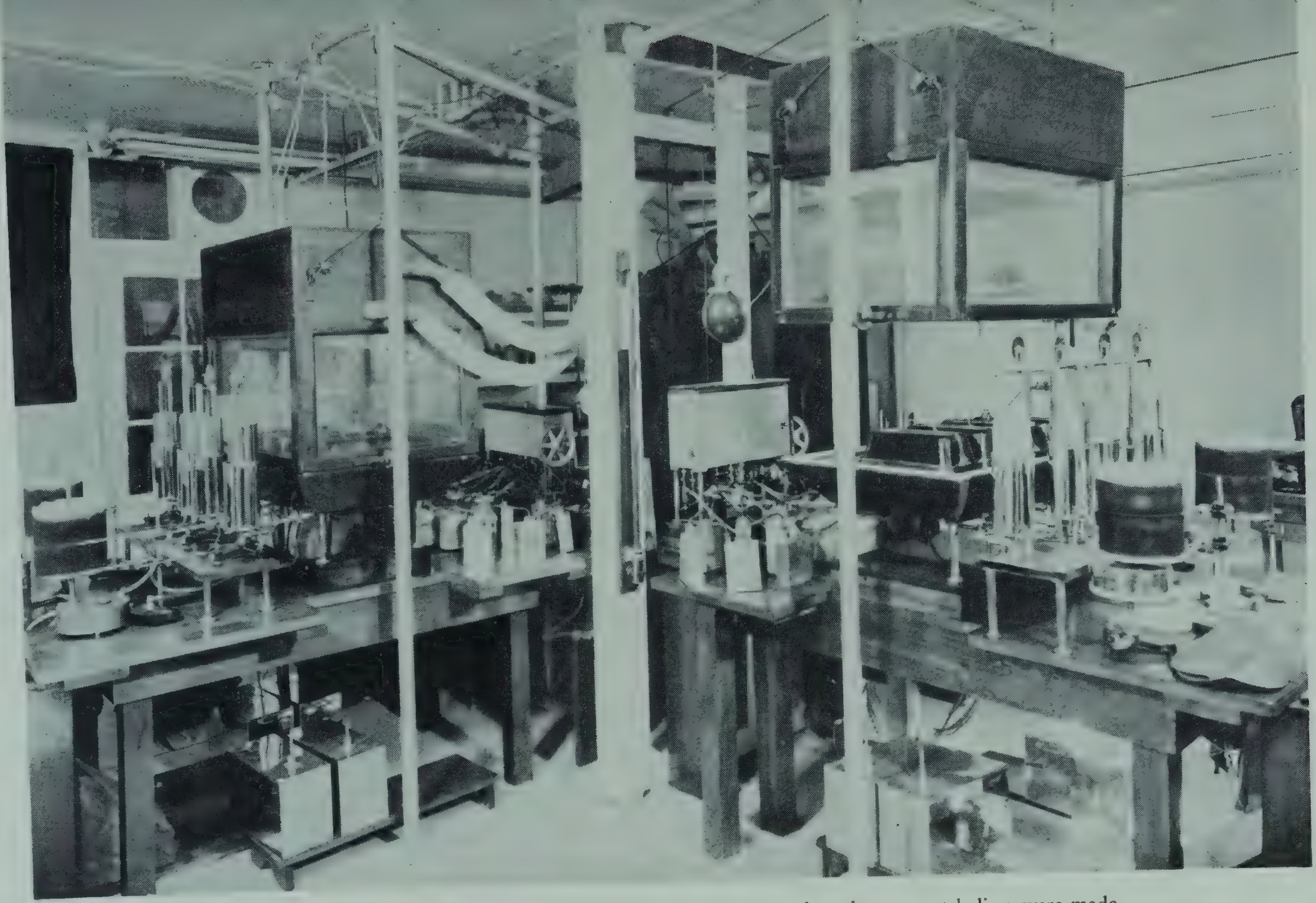
[2] Riddle, O., G. C. Christman, and F. G. Benedict, Amer. Jour. Physiol., 1930, vol. 95, p. 111.

[3] Benedict, F. G., Jour. Nutrition, 1930, vol. 3, p. 161.

[4] Benedict, F. G., and O. Riddle, Jour. Nutrition, 1929, vol. 1, p. 497.

PLATE 6



The apparatus in which all the present series of measurements of respiratory metabolism were made

obtained from them. The groups of birds selected were first examined to determine the food content of their crops; that quantity of food was increased by force-feeding (when necessary) to 5 gm. per 150 gm. body weight, and an equal amount of water was pipetted into their crops. The birds (usually 4 mated pairs) were then placed for 24 hours within the four compartments of a large glass cage (1 × 1 × 2 m.) which was maintained at the same temperature (within 1° C.) at which their rate of heat production was to be measured; for the first 2 to 3 hours spent in these compartments, the birds were further enclosed in very small cages (solid floors) in order that the occasional regurgitators of food could be identified. Water was kept before these birds until 4 to 6 hours before their removal from this large glass cage.

Twenty-four hours after these birds were fed (5:00 to 8:00 P.M., according to season), they were placed in suitable wire enclosures, wrapped carefully in heavy towels to prevent change of temperature in transit, and transferred (a distance of 8 m.) to the chambers of the apparatus for measurement of rate of heat production. One hour was always allowed to lapse between this transfer and the beginning of measurements; when marked activity (kymograph records) was observed within this hour, the beginning of measurement was deferred for an additional half-hour. Thereafter, during 5 to 6 hours, an uninterrupted series of independent measurements were made on each bird. Measurements were made only at night with the birds kept in completely darkened chambers. The time required to consume one pumpful (370 ml.) of oxygen constituted a "period," and, depending on the size of the bird, six to twelve periods were obtained for each bird. Only periods which were free, or practically free, from associated activity of the bird were used to determine the bird's rate of heat production. The average of the two (or three) lowest values thus obtained was taken as the correct measure of the bird's heat production. Calories were calculated from the amount of oxygen consumed.

It seems advisable to consider a possible criticism founded on the view that the metabolism of pigeons and doves measured after the twenty-fourth hour of fasting is abnormally low for comparison with the metabolism of other animals or with the metabolism of man measured at the twelfth hour of fasting. It might be urged that the reason for this low metabolism is that these small animals have an intense metabolism, hence draw rapidly upon their body stores, and in 24 hours reach a stage of fasting corresponding to a more prolonged fast in man and other animals. Against this argument may be adduced the facts that the metabolism of these birds, when quiet, is not intense (as shown by the study conducted for this purpose); that doves and pigeons digest and absorb ingested food much more slowly than does man; and that fat quotients are not obtained with these animals until at or near the twenty-fourth hour of fasting.

One may therefore conclude that in the dove and pigeon the metabolism prevailing at 24 hours after the ingestion of food has not been unduly lowered either by undernutrition or by pure fasting. Certainly, the degree of fasting which was uniformly used in the present study does not mean that the basal values obtained were thus forced to lower levels than are suitable for use in comparative physiology. Adequate preliminary tests fully warranted the use, as the standard condition for basal metabolism measurements with pigeons or doves, of a period beginning 24 hours after the last food. This necessarily assumes that the fasting shall be deemed to begin immediately following a period of food intake, and that at the hour the fast is begun the dove's crop contains 5 gm. (and the pigeon's crop 10 gm. per 300 gm. of body weight) of mixed grain, and a nearly equal amount of water. It presupposes also that this food is not regurgitated, and that during the fast the bird is not extraordinarily active, and is maintained at the same temperature (15°, 20°, or 30° C.) at which its heat production is to be measured.

The technique described above constitutes a part of the results obtained in a cooperative research with Dr. Francis G. Benedict, then Director of the Nutrition Laboratory of the Carnegie Institution, Boston, Massachusetts. The several additional investigations on dove and pigeon metabolism in which Dr. Benedict collaborated will be cited later, along with the other literature relating to special topics discussed in subsequent chapters.

The Relation of Heat Production to Weight and Surface

For the main purposes of the present study, the data on heat production could be calculated equally well in terms of body weight or in terms of body surface; for subsidiary purposes, however, it would be useful to know whether comparisons between doves and pigeons, and between small and large breeds of pigeons, are better made on the basis of surface than of weight. A large and more important segment of our data were obtained on ring doves and their hybrids. Size differences in this material are relatively insignificant. For all these birds weight was determined accurately; any calculation of body surface for any of them would involve an error of undetermined magnitude. All the data for doves are therefore presented in terms of calories per kilogram per hour. Our secondary interests nevertheless require that we consider the merits of expressing the results in terms of surface area, and that is done in the following pages.

Early in the history of studies on heat production it was recognized that the metabolism of animals per unit weight is inversely proportional to their size; or, stated differently, the metabolism of animals increases more slowly than their body weight. The relation was found to hold systematically, not only for different species, but for adult dogs of large and small size[5] and for rabbits of different sizes.[6] Results such as these led to the formulation of the surface law, which states that the basal metabolism of animals of different size is approximately proportional to their respective body surfaces. This law was first postulated in 1839[7] and was later advocated by others, largely on theoretical grounds. It was given little experimental support, however, until Rubner made accurate determinations of respiration in animals.

[5] Rubner, M., Ztschr. f. Biol., 1883, vol. 19, p. 535.

[6] Richet, C., La chaleur animale (F. Alcan, Paris, 1889).

[7] See historical review *in* Harris, J. A., and F. G. Benedict, A biometric study of basal metabolism in man (Carnegie Inst. Wash. Pub. 279, 1919).

In the application of the surface law various investigators found that the direct measurement of body surface was difficult and subject to considerable error. Various formulas were therefore devised for estimating the surface area from the weight and dimensions of the body. One of the first of these, attributed to Vierordt (Meeh, 1879[8]), gives the body surface as the ⅔ power of the body weight (this expresses the relative surface of similarly shaped bodies of different volume) multiplied by a constant K for the species in question. The "linear formula" of D. Du Bois[9] is based on measurements of various bodily dimensions (trunk, limbs, etc.) of several human subjects; this formula seems to be quite accurate even when applied to people differing greatly in body form. Later Du Bois and Du Bois[10] proposed a simplified formula for man which makes use of height and weight only, together with a species constant. This height-weight formula has come into general use in the study of human metabolism, and has necessitated only slight changes in the value of the exponents of H and W, and in the constant, to meet the requirements of particular age groups or nationalities (see E. F. Du Bois[11]).

The validity of the surface law has been questioned by many physiologists. While recognizing the value of such a principle for reducing all metabolic measurements to a common basis for comparison in animals of different size, these critics would avoid any implication of a causal relation between body surface and metabolism. Benedict was among the first to criticize the law, although admitting that it may have an empirical application to different species of animals. Harris and Benedict[7] made a statistical analysis of the metabolism of 239 adult human subjects and of 94 infants. It was from their measurements that many of the subsequent discussions of human metabolism originated, and upon them that earlier metabolic standards were largely based. The value of their work lies in the fact that, from a large amount of reliable data, they derived formulas by purely statistical methods which most clearly predicted the metabolism of their subjects; it is therefore not influenced by any theory of metabolism. Making extensive use of correlation coefficients, they came to the conclusion that human metabolism does not conform to the surface law. Others have since found, however, that results of metabolism plotted from the formulas of Harris and Benedict closely parallel those obtained from surface-area calculations.

In later work, on adult animals of different species, Benedict and his associates found that the basal metabolism, according to surface area, was fairly uniform except in some of the largest and smallest forms. It was distinctly higher in horses and cattle, and somewhat lower in the mouse, than the average level for all the species. For interspecific comparisons some investigators have used the Meeh type of formula, in which a different value of K was calculated for each species from surface measurements. The minimal value of K, for a spherical body, is 4.83; it is proportionately larger for more elongated bodies, and this applies to animals as well, whether they have a more linear form as in the snake or have elongated limbs as in the macaque. Benedict[12] determined the values of K for twenty three species of cold-blooded and warm-blooded vertebrates, and found that they vary from 8.4 for the sheep to 12.5 for the snake (with one unusual result, 57.5 for the bat). At that time he was of the opinion that the various factors (K) for different species are nearly enough identical, except in the case of a few aberrant forms, to warrant the use of a single value, 10; and that, for such comparisons, we may confidently discard all references to body surface itself and use only this factor and the $^{2}/_{3}$ power of the body weight for the calculation of the metabolism. That formula was adopted in the present study for making a few calculations (heat-production values at 30° C.) which thus permit a comparison of ring doves with large and small breeds of pigeons on the basis of calories per square meter of surface. It is possible that all data for pigeons, which vary markedly in size, should have been calculated on this or a similar basis. As noted elsewhere, however, weight was determined accurately, whereas any use of surface area would involve an error.

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[8] Meeh, K., Ztschr. f. Biol., 1879, vol. 15, p. 425.

[9] Du Bois, D., and E. F. Du Bois, Clin. Cal. 5, Arch. Internal Med., 1915, vol. 15, p. 868.

[10] Du Bois, D., and E. F. Du Bois, Clin. Cal. 10, Arch. Internal Med., 1916, vol. 17, p. 863.

[11] Du Bois, E. F., Basal metabolism in health and disease (3d ed., Lea & Febiger, Philadelphia, 1936).

E. F. Du Bois[11] has discussed the theories of metabolism in relation to the formulation of the surface-area law of Rubner. He points out that the original conception of metabolism as determined by heat loss underwent a change, and that Rubner himself modified his earlier views regarding the surface law. Physiologists generally have held to the belief that, although metabolism is often or usually in proportion to body surface, it is not causally related to it. There has been a change of attitude, according to Du Bois, because of our better knowledge of the physics of heat loss. Bohnenkamp[13] distinguished between total body surface and the "projection" surface, which amounts to approximately 80 per cent of the former and is responsible for loss of heat by radiation; he also emphasized the importance of subcutaneous fat in modifying the skin temperature and indirectly the radiation of heat. The recent investigation by Hardy and Du Bois[14] and their associates on heat production by men and women has an important bearing on this point (chapter 15).

Several writers have referred to the inaccuracy of surface-area determinations, resulting from stretching of the skin, from differences in method, and from the peculiarities of the species studied. Brody[15] called attention to some measurements of surface area in the albino rat, made independently by three investigators. The results, which he plotted for comparison, show an average difference between two of the sets of measurements of more than 60 per cent. He asks, "What is the use of relating metabolism to a unit of reference which varies by over 60 per cent when measured by different investigators? Why not relate it to weight which can be measured uniformly by all workers with a precision which is greater than 99 per cent."

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[12] Benedict, F. G., Asher-Spiro Ergebn. d. Physiol., 1933, vol. 36, p. 300.

[13] Bohnenkamp, H., and H. W. Ernst, Pflügers Arch. f. d. ges. Physiol., 1931, vol. 228, p. 41, p. 125; Bohnenkamp, H., Asher-Spiro Ergebn. d. Physiol., 1932, vol. 34, p. 848.

[14] Hardy, J. D., and E. F. Du Bois, Proc. Nat. Acad. Sci., 1940, vol. 26, p. 389.

[15] Brody, S., W. C. Hall, A. C. Ragsdale, and E. A. Trowbridge, Missouri Agric. Exper. Sta. Res. Bull. 166 (XVII), 1932.

Since only a small percentage of metabolism determinations are based on actual surface measurements, as contrasted with calculations of surface by arbitrary methods, some physiologists consider it desirable to have some other basis of reference, such as body weight. Thus one can avoid the assumption of a causal relation between body surface and heat production. Kleiber[16] compared the metabolism of thirteen groups of birds and mammals representing eight species, calculated according to their surface and according to various powers of their body weight between 0.67 and 1.0. From his analysis he concludes that the greatest uniformity of results is obtained when the metabolism is computed from the weight raised to a power of 0.73 or 0.74. The metabolism is higher in large species (especially in ruminants) than in small species according to surface or to powers of weight below 0.73, and is lower when calculated according to weight raised to a power greater than 0.75. Kleiber drew the further conclusion that a simple equation characterizing the metabolism by three coefficients (sex and species, age, specific stature) gives a prediction of the metabolism in man on the basis of the ⅔ or ¾ power of body weight which is as accurate as that obtained from the empirical regression equation of Harris and Benedict; moreover, Kleiber states that his equation is probably applicable to all homoiotherms of the same and of different species. Brody and Proctor[17] found that the basal metabolism of adult mammals and birds increased on the average with the 0.685 power of the body weight, varying between 0.64 for "wild" birds and 0.734 for mammals and the domestic fowl. The latter figure corresponds closely to the exponent in Kleiber's "best" power equation relating metabolism to body weight.

In his most recent comparative study Benedict[18] has included mammals ranging in size from the 8-gm. "dwarf" mouse to the 3700-kg. elephant, and birds from 17 gm. to 126 kg. in weight. He concludes that the surface law does not apply to the majority of the species studied; and that this law does not hold as between species differing greatly in size. For intraspecific comparison, the heat production of large and small individuals of a species per square meter of surface area was plotted against body weight, and in only nine out of twenty-two species did these give horizontal lines indicating close proportionality between metabolism and body surface (as in man, rat, and goose). In some species the line had a distinct upward slope (e.g., pigeon and dove), in others a downward slope (dog). The variation in the slope of these lines, indicating lack of conformity to the surface law within species, throws doubt upon the physiological basis of this law, according to Benedict. The plotted results for the different species show a general trend upward along the line representing the daily heat production per square

[16] Kleiber, M., Hilgardia (California Agric. Exper. Sta., Berkeley), 1932, vol. 6, no. 11.

[17] Brody, S., and R. C. Proctor, Missouri Agric. Exper. Sta. Res. Bull. 166, 1932.

[18] Benedict, F. G., Vital energetics (Carnegie Inst. Wash. Pub. 503, 1938).

meter of body surface, from the smallest to the largest. A rise from 278 calories in the dwarf mouse to 2060 calories in the elephant is indicated; or, from about 500 to 800 calories in mice and small birds, to values lying between 900 and 1900 calories in the goose, swine and cattle (both sexes), the pony, and the Percheron mare.

Benedict stressed the importance of comparing directly the total metabolism of species of the same average weight, whenever possible, to eliminate the weight factor. Thus he showed that the rabbit's metabolism is about 6 times, and the nonhibernating marmot's metabolism 4 times, as great as that of a rattlesnake at 37°. In a goose of the same weight it is 14 times as great as in the snake. He also sought, among the various formulas, to find the one which would serve best to equalize the basal metabolism in twenty-nine well measured groups of birds and mammals. The least variation in results was obtained when metabolism was related to the 0.73 power of body weight; there were large deviations from the mean, however, in atypical forms (dwarf mouse, marmot) and in others. Results calculated from Brody's formula ($Q = 70.5M^{0.734}$), giving total metabolism as a power function of body weight M, showed the following percentage deviations from the measured metabolism: for dwarf mouse +104, marmot +92, goat (doe) +22, rabbit +21, Percheron −27, canary −31, bull −36. According to Benedict these comparisons serve to emphasize the existence of difference, rather than similarity, in the metabolism of different species. It is his belief that no unifying principle has yet been devised to express metabolism. Although he believes that the surface law may not have interspecific application, yet he regards its continued use within certain species, especially man, as justified by experience and as valuable for stimulating investigation into the causal factors involved.

The tendency on the part of some investigators to stress mathematical formulation of the results of metabolism in terms of some power of body weight has diverted attention from the surface concept. But, as Benedict[18] says (p. 174), "unfortunately it has not emphasized the all-too-patent fact that the power function deals with the general law of growth and that consequently a heat-producing mechanism would normally be expected to develop much as the organism itself develops." This statement applies equally well to the various attempts to relate metabolism to the development of organs in the body, for, as Dreyer and his associates[19] found, the blood volume, cross section of the aorta, and cross section of the trachea in animals of different sizes are all proportional to $W^{\frac{2}{3}}$.

The several preceding considerations provide at least a partial justification for calculating and presenting all the present data in terms of body weight; and likewise for the use of the formula $S = 10 \times W^{\frac{2}{3}}$ in the special tabulation (table 13) which considers surface area in a comparison of heat production in the smallest and largest breeds here under discussion. The data of this table are calculated as heat production in calories per square meter per hour. It may be noted that, on a 24-hour basis, the average value obtained for a typical dove (race 63, body

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[19] Dreyer, G., W. Ray, and E. W. A. Walker, Proc. Roy. Soc. (London), B, 1912, vol. 86, p. 56.

TABLE 13

Heat production as calories per square meter per hour, in various races and hybrids of pigeons measured at 30° C. The value given is the mean obtained for the four seasons. Races are listed in the order of the magnitude of their heat production (in males).

Race or type	Males			Females		
	Number	Calories	Body weight (gm.)	Number	Calories	Body weight (gm.)
White King	12	31.40	577.7	9	32.58	553.6
Runt × Homer	26	28.45*	444.0	17	32.45	440.0
Homer	40	29.45	391.0	32	30.18	355.0
Runt × SA-E	24	28.07	437.0	22	30.19	412.0
Homer × Tippler	22	28.58	330.0	12	29.39	315.0
Runt × Homer C	37	28.35	463.0	10	29.31*	459.0
Runt	31	28.45	520.0	21	28.74	514.0
Runt × Magpie	17	28.00*	440.0	11	28.57	366.0
Tippler × SA-E	10	27.41	292.4	11	27.96	253.4
SA-R	41	27.29	334.3	25	28.05	323.0
Magpie × Tippler	13	27.08	288.0	..	.....	.....
SA-E	15	26.94	303.4	15	28.20	286.3
Tippler × 267	21	26.31	322.1	19	28.16	298.5
Tippler	71	25.93	270.7	67	27.91	264.9
Dove race 63	28	24.14	141.3	30	26.18	140.0

*Only three of the four seasons are represented in this average.

Magpies were not measured in winter (see table 53); they are especially elongate (tall) birds, and are omitted from this list.

weight 141 gm.) was 604 calories; for Tippler pigeons (weight 268 gm.), 646 calories; and for White Kings (weight 566 gm.), 768 calories. The relation of these (and some of the other) values to the respective body weights suggests that a value nearer to the ¾ power of the body weight might preferably have been used in these calculations.

Diurnal Rhythms in Heat Production

A recent and extensive review of the literature dealing with the subject of diurnal and activity rhythms was prepared by Herring and Brody.[20] Diurnal variations in metabolism, such as occur in man and certain animals, seem to be associated with day-and-night differences in activity, feeding, and body temperature. Even in the fasting animal in a resting state there is found a metabolic rhythm, attributed to variations in tonicity of the postural muscles, which is maintained reflexly by the diurnal light stimulus. According to the prevailing theory, the typical diurnal cycle is acquired, at some time after birth, as a conditioned reflex in response to activity and sleep. Rhythms of short duration, characterized by alternating periods of activity and sleep, are present in the young of many animals and in the human infant. These are supplanted by the longer diurnal rhythms in the majority of species, or they may persist into adult life in a few cases (rabbit, albino rat).

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[20] Herring, V. V., and S. Brody, Missouri Agric. Exper. Sta. Res. Bull. 274, 1938.

It has been shown[21] in fowl, however, that there is an inborn diurnal rhythm of basal metabolism, with a variation in amplitude, in chicks 1 week after hatching; the variation at this period is more than twice as great as that found at the age of 14 weeks. Light is the primary stimulus in the diurnal rhythm, acting indirectly by determining the habits of sleep. Although attempts to invert the daily rhythm of body temperature have not been entirely successful in man, this has been accomplished in animals, notably in domesticated birds. The persistence of the rhythm for some time during exposure to continuous light or darkness suggests that a periodic activity of the nervous system is involved. The physical factors contributing to the maintenance of the body-temperature rhythm, including possible cosmic influences, are discussed by Deighton.[22]

In man, and in animals which are active by day and sleep at night, the body temperature and metabolism are lowest during the night or the early morning hours (man). Nocturnal animals have a minimal body temperature in the daytime; also, the lowest basal metabolism was obtained in daytime in the rat. Herzog[23] found some, though inconclusive, evidence of a nocturnal increase in the metabolism of an owl. Lee[24] was unable to find any diurnal difference in the basal metabolism of the rabbit.

It is well known that there is a diurnal rhythm of voluntary activity in the rat, with periods of rest during the day and greater activity at night.[25–27] The fasting metabolism has also been found[20, 28] to be lowest during the middle of the day. The activity could be reduced by continuous light, but the metabolic rhythm continued, apparently because of variations in muscle tone.[20] This rhythm was not extinguished by the continuous action of light alone, nor by continuous feeding alone, in the course of a month; it disappeared in a week, however, under the combined influence of these two factors.

A distinct diurnal rhythm of metabolism has been observed in the domestic fowl. This was first demonstrated in the cock.[29, 30] Herzog[23] found that the basal heat production of hens, pigeons, and male geese was about 17 per cent higher during the daytime than at night, and that of the cock 25 per cent higher, but that that of female geese and ducks was only 5 and 8 per cent higher, respectively. More recently it was reported[31] that the fasting heat production of Light Sussex cockerels was about 9 per cent higher in the morning than it was at night. A diurnal variation was also found[32] in the basal metabolism of Rhode Island Red hens, with a maximum rate at 8:00 A.M. and a minimum at or near 8:00 P.M.

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[21] Barott, H. G., J. C. Fritz, E. M. Pringle, and H. W. Titus, Jour. Nutrition, 1938, vol. 15, p. 145.

[22] Deighton, T., Physiol. Reviews, 1933, vol. 13, p. 427.

[23] Herzog, D., Wissensch. Arch. f. Landwirtsch., 1930, vol. 3, p. 601.

[24] Lee, R. C., Jour. Nutrition, 1939, vol. 18, p. 473.

[25] Richter, C. P., Comp. Psychol. Monogr., 1922, vol. 1, p. 55.

[26] Richter, C. P., Quart. Rev. Biol., 1927, vol. 2, p. 307.

[27] Slonaker, J. R., Amer. Jour. Physiol., 1925, vol. 71, p. 362; 1925, vol. 73, p. 485.

[28] Horst, K., L. B. Mendel, and F. G. Benedict, Jour. Nutrition, 1934, vol. 7, p. 277.

[29] Bacq, Q. M., Ann. de physiol., 1929, vol. 5, p. 477.

[30] Terroine, E. F., Ann. de physiol., 1929, vol. 5, p. 842.

Benedict and Riddle[33] found that the metabolism of doves and pigeons, under basal conditions and in almost continuous darkness, was 15 per cent greater in the daytime than at night. Others[34,35] have observed a somewhat greater difference in pigeons. A diurnal rhythm in metabolism was observed at low temperatures as well as at thermal neutrality. The metabolic rate was lowest during the early part of the night, after which it rose gradually to a maximum in the middle of the day.

Since measurements made in the present study usually extended over the period from 7:00 P.M. to 1:00 A.M., it is evident that the values obtained are close to the minimum values imposed by the daily rhythm.

[31] Deighton, T., and J. C. D. Hutchinson, Jour. Agric. Sci., 1940, vol. 30, p. 141.

[32] Barott, H. G., and E. M. Pringle, Jour. Nutrition, 1941, vol. 22, p. 273.

[33] Benedict, F. G., and O. Riddle, Jour. Nutrition, 1929, vol. 1, p. 497.

[34] Burchard, E., L. Dontcheff, and C. Kayser, Ann. de physiol., 1933, vol. 9, p. 303.

[35] Dontcheff, L., C. Kayser, and P. Reiss, Ann. de physiol., 1935, vol. 11, p. 1185.

13

THE ROLE OF RACE IN HEAT PRODUCTION

HISTORICAL

At an early but important stage in the development of this subject physiologists were dominated by the thought that the heat production of all warm-blooded animals is controlled by the surface area and that for each square meter of surface area the heat lost from the body amounts to about 1000 calories per 24 hours. According to this view, first stated by Rubner,[1] species difference, or even the difference between bird and mammal, did not or need not involve distinctions in rate of heat production. Numerous later investigations showed that metabolic rate is not the same in all species and that it may be affected by such things as sex, age, diet, and climate. Is *race* also a basis for difference in heat production? This question is of much importance in connection with the broader question of the reality, nature, and extent of genetic inequality among and within the tribes of man; it is of primary concern in this study of racial difference in doves and pigeons. The present status of the answer to the question of racial differences in heat production will now be considered with reference to (*a*) human races, and (*b*) races within other species.

In recent decades various national and racial groups have been studied extensively. A few summary statements by leading investigators on the significance of these studies should be quoted at once. Du Bois[2] has written as follows:

> In summarizing these results it seems clear that there are distinct racial differences in metabolism apart from the effects of climate. Native Australians show a low metabolism, Chinese slightly low, Japanese close to the American figures. Natives of certain parts of India and Syria are distinctly low, perhaps partly on account of differences in diet and muscular activity. The white inhabitants of Central and South America seem to show no racial divergences but perhaps a slight lowering due to the warm climate. On the other hand, the Maya Indians and Araucanians are well above the averages for whites in North America. No satisfactory explanation has been offered for the racial differences. There is no reason to assume any particular superiority in a higher average of metabolism or inferiority in a lower average.

The present writer has noted (see Steggerda and Benedict)[3] that there are reasons for believing that the high metabolism of Maya (and Araucanian) Indians is ascribable to hyperthyroid activity induced by the habits of these peoples, or by climatic exposure, or by both. Certainly these sources of high rates of heat production have not been excluded.

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[1] Rubner, M., Ztschr. f. Biol., 1883, vol. 19, p. 535.

[2] Du Bois, E. F., Basal metabolism in health and disease, p. 200 (3d ed., Lea & Febiger, Philadelphia, 1936).

[3] Steggerda, M., and F. G. Benedict, Amer. Jour. Physiol., 1932, vol. 100, p. 274.

Benedict,[4] after several separate studies on racial groups, drew the following conclusions:

> A survey of the basal metabolism of numerous races of humans has been made in the past ten years by the Nutrition Laboratory and its various collaborators, with emphasis upon Chinese (both those born in the United States and those in China), South Indian women, Maya Indians in Yucatan, and mixed races in Hawaii. . . . As the Nutrition Laboratory's survey was based upon the use of a single technique, carried out by well-trained investigators, the results are strictly comparable. Even when allowances are made for differences in temperament (Oriental placidity versus Occidental tenseness) and for inexperience in serving as subjects of metabolism measurements, it is clearly shown that Oriental races in general have a metabolism somewhat lower than that of Caucasians in the United States. The South Indian women in Madras have a very low metabolism (17 per cent below the Caucasian prediction standards), and this is further depressed about 10 per cent during deep sleep. Researches from other laboratories have given varying results. In striking contrast to the low metabolism of the majority of the Oriental races is the high metabolism of the Maya of Yucatan. The Indians in Chile have likewise been found by Dr. Pi Suner to have a high metabolism. Twenty-four Miao males in Szechwan, China, have been demonstrated by Dr. Kilborn to have a metabolism 16 per cent above the Caucasian prediction standards, accompanied by a low pulse rate of 55 beats per minute. To the well-known factors affecting basal metabolism—weight, height, age, and sex—must now be added a fifth factor, race.

The most recent of these statements, and the one best expressing present doubt and difficulties concerning the question of racial differences in humans, is given in a review article by Carpenter:[5]

> Evidence is accumulating that the deviations in the basal metabolic rates of racial groups from the normal Caucasian standards are not ascribable primarily to actual racial differences. The metabolism of races is usually affected by so many other factors, such as climate and diet, that it is difficult to arrange a study in such a way that the factor of race is the only one exerting an influence.

The importance of the climatic factor is indicated by Forbes and Voris[6] in a summary of recent researches on Oriental races in Java:[7]

> The metabolic rate of normal male Chinese and natives at Sourabaia averaged 9 per cent below the standard of Boothby, Berkson and Dunn (Mayo). Since normal male Europeans in Batavia showed a similar reduction of basal metabolic rate, this reduction was not racial, but was due, in the main, to the tropical environment.

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[4] Benedict, F. G., Proc. Amer. Philos. Soc., 1937, vol. 78, p. 101.

[5] Carpenter, T. M., Ann. Rev. Physiol., 1941, vol. 3, p. 131.

[6] Forbes, E. B., and Le R. Voris, Ann. Rev. Physiol., 1943, vol. 5, p. 110.

[7] Streef, G. M., and R. Karmawan, Geneesk. Tijdschr. Ned.-Ind., 1942, vol. 82, p. 72; Biol. Abstracts, vol. 16, p. 1522.

Recent studies of Crile and Quiring[8] on American aborigines are to be noted. They reported that in Chippewa Indians of northeastern Canada, the average basal metabolism of 4 males was +18.0, and that of 6 females +18.5 per cent, according to the Mayo standards. It was found in Eskimos to be +14.5 for 28 males, and +21.1 for 24 females. Excluded from these averages are several values greater than +40 per cent. They also found[9] for Maya Quiché Indians an increase of 8.2 per cent in 30 soldiers stationed at an altitude of 8100 feet in Guatemala; and an increase of 5.2 per cent in 5 plantation laborers at 800 feet elevation. It should be noted, however, that 32 of 33 of the Maya subjects examined by Crile showed evidence of diffuse endemic goiter. These authors refer also to an extensive study made on Navajo Indians by Dr. C. G. Salsbury, who stated (in personal communication) that in 1136 tests the average basal metabolism was +2.4 per cent. For 10 Eskimos Rabinowitch and Smith[10] reported that the average basal metabolism was +26 per cent.

Certain rather special cases of racial difference in animals have been observed. The pigeon mutant "scraggly," characterized by slight and very defective plumage, was briefly noted[11] to have a rate of heat production distinctly higher than that of other breeds of pigeons. Complete data concerning this race will be presented in this volume. The "frizzle fowl," which is likewise provided with plumage which permits too rapid loss of heat, was found[12] to have a higher rate of heat production than other races of fowl. The "hairless" albino mouse was shown[13] to have a somewhat higher basal metabolism than the normal mouse when each type was measured at its critical temperature; this temperature was 34.0° C. for the hairless and 28.5° C. for the normal mouse. The "hairless" albino rat was likewise found[14] to display a higher metabolism. In all this group of cases the increased heat production apparently serves as a compensation for greater heat loss from the body due to inadequate body covering; this latter, in turn, is under definite genetic control. Moreover, continuously poor protection against heat loss probably implies continuously increased thyroid activity such as occurs only in cold weather in normally clad birds and mammals. Since, in at least some of these cases, only a single recessive gene separates the poorly insulated types from normals, these mutant types are not strictly comparable with human races; they are more nearly comparable with occasional teratologies that may occur within all races.

Some evidence for racial differences in basal metabolism has been obtained in strains of laboratory and domesticated animals, but only in a few cases are these differences either large or definitely established. For the mouse, the diverse results given in the literature suggest that racial factors may be operative, but it seems more likely that many of the observed differences resulted from uncontrolled activity (and small size) of this animal. Benedict and Fox[13] pointed out that the mouse is constitutionally the least suitable animal for measurement of basal metabolism. In a review of published data on the mouse they called attention to the wide diversity in the results of other investigators for daily heat production per square meter of surface, ranging from 555 to 2736 at medium temperatures. From determinations[15] on 4 strains of mice, made under identical conditions and calculated per unit surface or unit weight, a much lower basal metabolism was found in the hereditary (pituitary) dwarf than in the white, the fat, or the wild mouse. There were smaller differences among the last three strains, one difference being a slightly lower metabolism in the white than in the wild mouse. In a later study[16] of the dwarf mouse, a form which has a rudimentary thyroid through lack of the gene necessary for development of eosinophilic cells in its pituitary,[17,18] it was found that the rate of oxygen consumption per unit area was 30 to 40 per cent lower than in the normal mouse. During the earliest stages of growth the metabolic rate was the same in both types, but after the first week it failed to rise as rapidly in the dwarf as in the normal; this latter period was coincident with a retarded rate of growth in the dwarf.

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[8] Crile, G. W., and D. P. Quiring, Jour. Nutrition, 1939, vol. 18, p. 361.

[9] *Ibid.*, p. 369.

[10] Rabinowitch, I. M., and F. C. Smith, Jour. Nutrition, 1936, vol. 12, p. 337.

[11] Benedict, F. G., and O. Riddle, Jour. Nutrition, 1929, vol. 1, p. 497.

[12] Benedict, F. G., W. Landauer, and E. L. Fox, Storrs Agric. Exper. Sta. Bull. 177, 1932, p. 13.

[13] Benedict, F. G., and E. L. Fox, Pflügers Arch., 1933, vol. 231, p. 455.

[14] Schopback, R. R., C. E. Keeler, and H. A. Greenberg, Growth, 1943, vol. 7, p. 83.

Concerning racial differences in the rat, comparatively little is known. Albino rats were found[19] to have a distinctly lower basal metabolism than recently captured wild gray Norwegian rats. In a comparison[14] of Wistar albinos with an inbred strain of gray Norwegian rats and their F_2 hybrids, under nembutal anesthesia, the albinos were shown to have a somewhat higher rate of metabolism. The effect of confinement in depressing the basal metabolism of wild animals may have been reflected in these results.

Very few comparative studies have been reported which deal with the metabolism of different breeds of cattle or other ruminants. Owing to the technical difficulties encountered in work with large ruminants, and the lability of their metabolism—well illustrated by investigations on the cow—the evaluation of basal heat production measurements is often a matter of uncertainty. In one investigation[20] a comparison was made between Jersey and Holstein cows, ranging in age from 3 to 15 years, but having a comparable average age for each breed (about 9 years). The basal heat production (fourth and fifth days of fasting), in calories per square meter per day, was found to be 1065 for 2 Jersey cows and 975 for 3 Holstein cows on a previous diet of hay; it was 1470 for 2 Jerseys and 1290 for 2 Holsteins on a previous diet of grass. Some recent nonbasal measurements were made[21] of the metabolism (after only 12 hours of fasting) of animals over 6 months old; 18 Jersey heifers gave a value of 2000 calories, and 15 similar Holstein heifers gave a value of 2142 calories per square meter per day.

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[15] Benedict, F. G., and R. C. Lee, Ann. de physiol., 1936, vol. 12, p. 983.

[16] Boettiger, E. G., Endocrinology, vol. 28, p. 785.

[17] Smith, P. E., and E. C. MacDowell, Anat. Rec., 1930, vol. 46, p. 249.

[18] Smith, P. E., and E. C. MacDowell, Anat. Rec., 1931, vol. 50, p. 85.

[19] Benedict, F. G., and J. M. Petrik, Amer. Jour. Physiol., 1930, vol. 94, p. 662.

[20] Ritzman, E. G., and F. G. Benedict, The nutritional physiology of the adult ruminant (Carnegie Inst. Wash. Pub. 494, 1938).

The basal metabolism of White Plymouth Rock hens was found to be 628 calories per square meter per day, compared with 703 calories for Rhode Island Red hens.[22] The authors considered it possible that a difference in degree of activity accounted for these results.

The behavior of metabolic rate in inheritance is practically unknown; this despite the fact that some measurements, such as those of Benedict[23] on browns and blacks in Jamaica, have been reported.

Experimental Results

All the large amount of tabular material presented in this chapter relates to the role of race and hybridity in heat production. The several subdivisions of the data of each table permit a separate consideration of such factors as season, sex, temperature at which measurements were made, and age; for reasons of convenience of description these particular factors will be considered in subsequent chapters. It is believed that the publication of the results of all measurements warrants the use of a minimum of description and discussion of the data obtained for the several races.

Data from Dove Races and Hybrids

Tables 14 to 43 (pp. 198–228) record average heat-production values and respiratory quotients. Despite the fact that nearly all the present data were obtained on birds fasted 24 hours, and respiratory quotients close to 0.72 were expected, values ranging from 0.79 to 0.84 were sufficiently frequent to render it advisable to make a permanent record of these measurements. Some types of pigeons yielded these high quotients in excess; more definite information on the source or cause of such quotients is not now available.

The relative order of heat production at 30° C. (basal values) in the various races and hybrids was presented in table 3 (p. 73), and the relation of some of the heat-production values to thyroid size was there noted. A similar listing of these races and hybrids according to their heat production at 20° C. is given in table 44 (p. 229). The most important single fact relating to actual heat production by the various types of doves—namely, the absolute value of the heat production in its relation to that of other types—is obtainable through inspection and comparison of the data of tables 3 and 44.

Heat production in these dove races seems more closely associated with thyroid type (see chapter 3) than with any other element of constitution examined in this study. Race *75* (table 14) had a higher basal metabolic rate (see table 3 for basal values) than any other race of doves, and it was otherwise characterized as the race having the smallest thyroids. In all cases (3 tests) in which race *75* was combined with another race, the resulting hybrids had a higher B.M.R. than that of the other race represented in the hybrid. Again, races *N2* and *51* had small thyroids; the thyroids of race *W* were not adequately measured, but apparently they were intermediate or large. These three races, following race *75*, had higher levels of basal heat production than any other dove races. Race *36* apparently provides an exception. Originally, at least, this race had relatively small thyroids; its rate of heat production was rather low.

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[21] Brody, S., H. H. Kibler, and A. C. Ragsdale, Univ. Missouri Agric. Exper. Sta. Res. Bull. 350, 1942.

[22] Mitchell, H. H., L. E. Card, and W. T. Haines, Jour. Agric. Res., 1927, vol. 34, p. 945.

[23] Davenport, C. B., and M. Steggerda, Race crossing in Jamaica, p. 281 (Carnegie Inst. Wash. Pub. 395, 1929).

In races characterized by largest thyroid size the B.M.R. tends to be low or intermediate in value. In race *B* (table 15) the metabolic rate is intermediate, and none of the hybrid types (table 3) containing race *B* (4 tests) had a lower metabolic rate than that of race *B*. Race *62* (table 17), with very large thyroids, had a very low rate of heat production. Race *72* (table 31) had only moderately large thyroids and its rate of heat production was low or intermediate. This race is represented in 8 of the hybrid types whose rate of heat production was adequately measured at 30° C.; all these hybrid types (table 3) also showed low or intermediate rates of heat production, except the two types in which races *75* and *B* were also involved, and these hybrids had a high B.M.R. It may be noted that race *G* (table 20) apparently had a surprisingly low rate of basal heat production, but the number of measurements is too small to warrant the inclusion of this race in the summaries given in tables 3 and 44.

Races *63*, *OT*, and *67* (the "miscellaneous" group perhaps belongs here) had thyroids of intermediate weight, and for these groups an intermediate or low rate of heat production was found.

In dove hybrids with extreme rates of basal heat production the relation of thyroid type to the metabolism is less evident. Hybrids *63* × *62* and *72* × *62* had very low basal rates and large thyroids; but other hybrids (*67* × *72* and *63* × *OT*) with low basal rates, like those (*NE* × *N2* and *44* × *N2*) with extremely high rates, had thyroids of intermediate size.

In this connection it may be noted that relative heart weight was exceptionally high in races *51*, *75*, and *72* and in hybrids *62* × *B*, *72* × *75*, *72* × *NA*, and *75* × *B;* it was exceptionally low in races *NA*, *N2*, and *63* and in hybrids *63* × *N2*, *11* × *62*, and *63* × *62*. Relative weight of feathers (observed in 8 races only) was apparently high in races *NA* and *OT;* it was apparently low in races *N2*, *51*, and *62*. These and related items are further discussed in chapter 16. Rates of heat production in these races are not consistently related to their relative responsiveness to prolactin (tables 4, 5). Nor are they generally thus related to either intestinal length (tables 7, 8) or pituitary size (table 9). It may not be a matter of mere chance, however, that the particular dove and pigeon races (race *75* and Magpies) which had the highest rates of heat production within their respective groups also had, in relation to body weight, the heaviest pituitary glands (tables 9, 10).

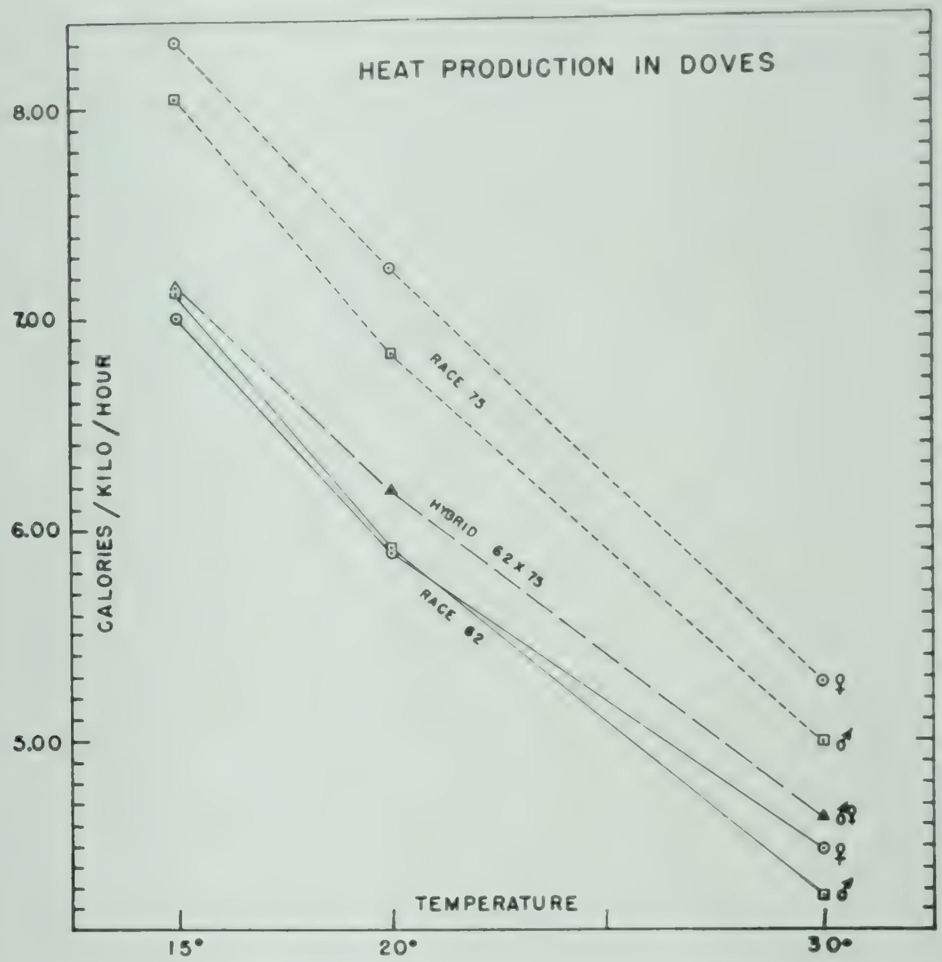

Fig. 173. Heat production in races *75* and *62* and in their hybrids

It was elsewhere noted (chapter 3) that the 4 races which stand at the top of the list in table 3 had rates of heat production from 10 to 17 per cent higher than the 4 races at the bottom of the list. As regards basal heat production, these data leave no doubt that distinct races of doves were segregated and established. It is to be noted that this result was obtained among types containing only *Streptopelia risoria* as well as among types which contained the blood of another species. Races *N2*, *W*, *B*, *67*, and *36* are pure *risoria*. It is also evident that the observed differences in the metabolic rate of these races are partly or largely associated with the type of thyroid which prevailed in them. Neither heart size nor feather weight seems to be closely or consistently associated with basal heat production in the various groups of ring doves.

Both a confirmation of the above conclusions and some additional facts were obtained from measurements made at 20° C. (table 44) on essentially this same series of races and hybrids. It will be noted that the same 4 types which head the four lists in table 3 also head the lists in table 44. Again, races *62* and *36* (also hybrids *67* × *72* and *63* × *62*) occupy very low positions on both lists. On the other hand, types such as race *N1* and hybrids *63* × *OT* were found to make a

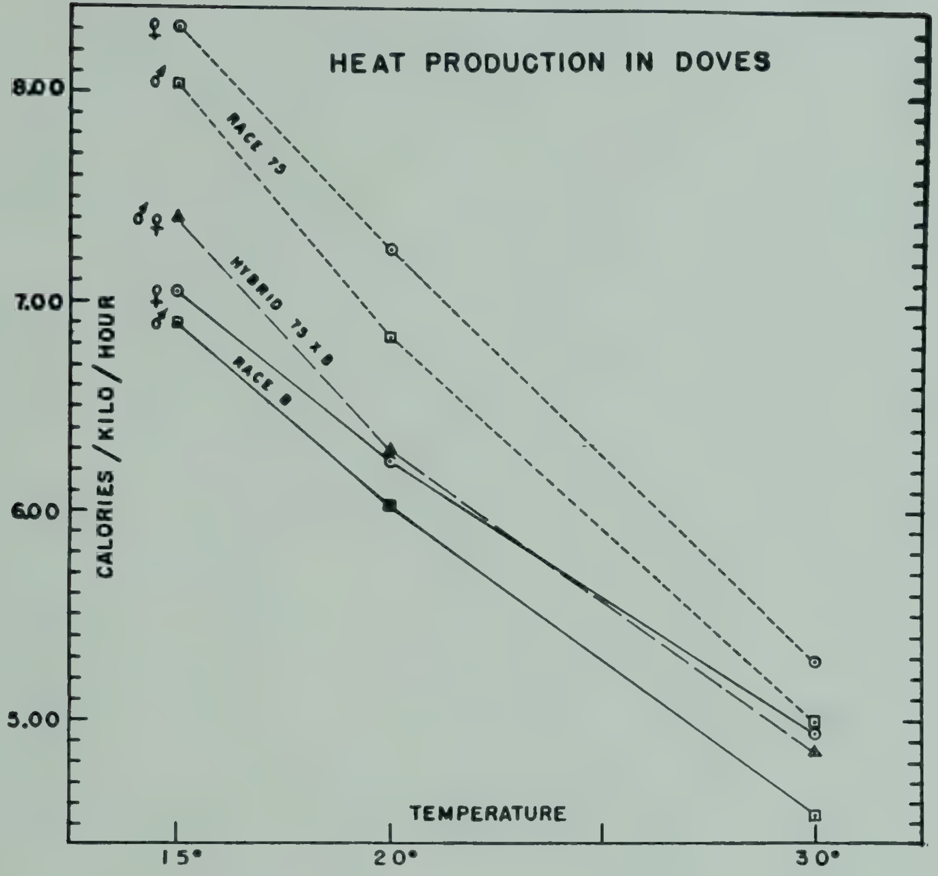

Fig. 174. Heat production in races *75* and *B* and in their hybrids

notably greater increase in their heat production at 20° C., over that at 30° C., than did races *62* and *36* and hybrids *11* × *62* and *36* × *N2;* and race *51*, which had high basal values (it also had slightly reduced body temperature and a low pituitary weight, and carried a genetic factor for myoclonus), responded notably less to the lower temperature than did races *75* and *N2*. Thus, some types give evidence of racial difference by responding unequally to changes in temperature, as well as by showing unequal basal values and (in some cases at least) by their ability to transmit that characteristic when outcrossed with another race. The presence of active myoclonus in some individuals of race *51* (table 29) seems not to have differentiated their rate of heat production from that of those members of the race which did not exhibit this trait. Curves describing heat production in races *75*, *B*, and *62*, and in two types of hybrids formed from these races, are shown in figures 173 and 174.

The data of tables 42 and 43 relate to the possible effect of nearness to ovulation (within 50 hours) on rate of heat production. Some females of all races and hybrid types were in this stage of reproduction when measured, and the data as a whole indicate that at this period the heat production is slightly increased despite the fact that in many of the measurements (those at 24 to 50 hours before ovulation) 2 to 4 gm. (about 1.0 per cent of the body weight) of a special nonmetabolizing tissue (yolk) was included in the body weight. Inclusion of data obtained from females at these periods means therefore that the racial averages listed in tables 3 and 44, and the yearly averages for all females (tables 14 to 40), are somewhat higher than would have been found for females in reproductive rest. Of greater significance is the question of the extent to which the observed sex differences are affected by the inclusion of values from these temporarily stimulated females. That matter is therefore fully considered in chapter 15.

Data from Pigeon Races and Hybrids

The results obtained on all types of pigeons are given in tables 45 to 64 (pp. 230 250). It is almost or quite impossible to gauge the extent to which the thyroid glands determined rate of heat production in most of the types of pigeons studied here. There are two major difficulties. In the first place, marked differences in form and size among these types render it impossible to know the exact extent to which heat production in one type actually differs from that in another. Calculations made on the basis of body weight (tables 3, 44) tend, with some exceptions, to assign high values to small types and low values to heavy types. Calculations (table 13) based on a widely used formula ($S = 10 \times W^{\frac{2}{3}}$) for deriving surface from body weight tend, with still fewer exceptions, to reverse the above-described order and assign highest values to the heaviest breeds. In the second place, thyroid weight was considerably affected by goitrogenic conditions which prevailed during most but not all of the period covered by these tests. Moreover, the measurements of thyroid size and of heat production were not made on the several pigeon types at entirely comparable periods.

In a restricted group of cases, however, the metabolic level is rather clearly associated with type of thyroids. Normal and ataxic members of races *SA-E* and *SA-R* had practically identical metabolic rates (tables 3, 44), and thyroid weight was low and nearly or quite indistinguishable within these groups; corresponding scraggly types differed in having heavier thyroids (35 to 40 per cent) and a higher rate of heat production. Even the thyroids of this latter group, however, were by no means of goitrous proportions; their median value was about 0.014 per cent of the body weight, whereas that of the normal type was about 0.010 per cent; thus the thyroids of these scragglies differed from those of their normal-type brothers by only the amount by which a pigeon thyroid in summer can be increased by exposure to cold.[24]

It is notable that relative heart weight was exceptionally high in types *R* × *HC*, *T*, *T* × *H*, and *M* × *299;* it was exceptionally low in *R*, *R* × *M*, and *R* × *SA-E*. Relative weight of feathers (observed in 6 types only) was high in Tipplers and *SA-E;* it was low in Magpies and in Runt × Magpie hybrids. These and related items are further discussed in chapter 16.

The relatively high metabolism of Magpies (table 53), and the ability of this breed to transmit this characteristic, are especially evident in measurements made at 20° C. (table 44). There, as in the 30° measurements (table 3), the Magpies head the list of races (except the partly naked scragglies); and they are also represented in all the 4 types which head the list of hybrids. Moreover, no hybrid containing Magpie blood is listed in a lower position in that table. It was noted above that relative size of the pituitary gland was greater in Magpies than in any of the other types of pigeons examined for pituitary weight (table 10).

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[24] Riddle, O., and W. S. Fisher, Amer. Jour. Physiol., 1925, vol. 72, p. 464.

Two or three items relating to technique or to factors affecting rate of heat production are to be found in the tabulated data. Since the rate of heat production is abnormally high in scraggly pigeons, and since these birds are of a very aberrant type with respect to their plumage, it is important to know whether 30° C. is or is not within the zone of thermal neutrality for birds of this type; that this is so is shown by the data of table 49. The great importance attaching to an adequate period of fasting, except perhaps for measurements made at very low temperatures, is indicated by data obtained on young Carneau pigeons (table 59). Incidentally, these data show that in these *young* pigeons minimal or basal values may be obtained at a temperature as low as 25° C. In general, this is not true for adult pigeons.

The effect of congenital blindness is recorded for a male Magpie in table 53 and for a female Tippler × *267* hybrid in table 52. When measured in adult but nonsenile stages the male Magpie had a lower rate of heat production (10 of 11 tests or series of tests) than the control males; when this male was 5 to 11 years old, however, its heat production exceeded that of the control in 3 series of tests and was less than that of the control in an equal number of tests. The female hybrid also had a lower metabolic rate (11 of 13 tests) when measured in adult but nonsenile stages; when it was more than 5 years old its rate exceeded that of the control in 1 test and was less than that of the control in 2 tests.

The Hybrid State and Heat Production

Preceding descriptions of the present material have laid little stress on the data obtained from hybrids. Questions concerning the mode of inheritance of the metabolic level would have required the subdivision of the data into values obtained on F_1, F_2, and F_+ hybrids. In general, the number of F_1 and F_2 individuals measured was too small to permit conclusions of value. On certain related topics, however, a brief statement is warranted.

Some special evidence that races with low or high metabolic rate tend to transmit this trait may be observed in figures 173 and 174, and in the lists provided in tables 3 and 44. The dove races (*75*, *N2*, and *51*) with highest basal metabolic rates (table 3) yielded hybrids whose metabolism tends to fall in the upper half of the lists of "hybrids" in tables 3 and 44. The three races (*62*, *36*, and *OT*) with lowest metabolic rates tended to produce hybrids whose metabolic rates place them in the lower half of these lists; for race *36*, however, this statement applies to measurements made at 20° C. but not at 30° C. The tendency of 4 types of Magpie hybrids to exhibit relatively high metabolic rates at 20° C. was noted on a preceding page.

The data for ring dove hybrids seem to provide little or no evidence that hybridity is, in itself, the source of change in metabolic rate. It has been made clear, however, that many or most of the parental races were rather closely related. The pigeon hybrids, though mostly from distinct breeds, usually differ considerably in body size from the parent races; and here the uncertainty concerning a valid method of computing the metabolism of birds of dissimilar size precludes a satisfactory solution of the problem on the basis of the present data.

Data from hybrids obtained by crossing the Tippler and dove—an extremely wide cross that produces only, or practically only, males—are given in table 41. All individuals of this group were F_1 hybrids. It will be observed that only at 20° C. was a suitable number of measurements made on these hybrids. The body weights (fasted) of the three types involved were: 153 gm. (dove), 194 gm. (hybrids), and 265 gm. (pigeon). Per kilogram per hour the values obtained for the three groups were 6.10, 5.49, and 4.45 calories, respectively. Per square meter per hour these values were 32.68, 31.79, and 28.58 calories, respectively. Though these data rather clearly suggest that heat production in the hybrids is intermediate to the values found for the parental races, significance may attach to the fact that the metabolism of the hybrid so closely approaches that of the parent (dove) whose metabolism is highest (and whose body weight is lowest).

CONCLUSIONS

Extensive study of rate of heat production in the races otherwise studied in part I of this volume has demonstrated that several of the segregated races of ring doves are characterized by unequal basal metabolic rates. The number of actually distinct metabolic levels within an apparently continuous series is unknown.

Dove races *75*, *N2*, *51*, and *W* were demonstrated to have high basal rates (measured at 30° C.). The heat production of these 4 races was 10 to 17 per cent higher than that of dove races *62*, *36*, *OT*, and *67*, whose basal rates were low. Races *63*, *B*, *N.1*, and *72* had basal rates intermediate to those of the above-named racial groups.

When measured at 20° C., all the 4 dove races which had lowest basals again showed the lowest rates of heat production, and 2 of the races (*75* and *N2*) with extremely high basals again showed highest rates; but in race *51* this decrease of temperature stimulated heat production much less than in race *N.1*. Thus, racial difference in heat production relates both to actual basal level and to inequality of response to a lowering of the temperature. Hybrid types of doves provided further illustrations of all the above-noted responses to measurement at 20° C.

Hybrids *NE* × *N2* and *44* × *N2* had very high, and hybrids *63* × *62* and *67* × *72* had very low, basal rates. When measured at 20° C. these types essentially retained their respective (and extreme) metabolic rates relative to rates obtained in all other hybrid types.

Basal heat production in dove races seems to be largely but not solely associated with thyroid type and function. Relative size of heart, intestinal length, responsiveness to prolactin, and weight of plumage were not associated in any consistent way with the basal heat production of dove races. It is possibly significant that relatively heaviest pituitary glands characterized both the dove race

(75) and the pigeon race (Magpies) which, in these two species, showed the maximum rate of heat production (at both 30° and 20° C.). Magpies are more elongate, and have relatively lighter plumage (less insulation), than other breeds of pigeons.

The presence of active myoclonus complexus in some individuals of race *51* did not measurably affect rate of heat production. This conclusion is based on the equality of values obtained in affected and unaffected members of the race.

Uncertainties attending methods of calculating heat production in pigeon breeds of very unequal size now prevent valid conclusions regarding relative rates of heat production in several of the types of pigeons included in this study. Calculations based directly on body weight assign lower values to the larger breeds, whereas calculations based on the formula $S = 10 \times W^{\frac{2}{3}}$ tend to assign higher values to the larger breeds.

Among pigeons the abnormal (partly naked) scragglies have the highest metabolic rate. Of the 4 or 5 normal types in which the body weight is small and relatively uniform, metabolic rate was apparently highest in Magpies. The extent to which thyroid type and other factors are associated with rate of heat production is discussed. In race *267* (the source of the "hermaphrodite-producing" race), low thyroid weight and a low rate of heat production were apparently associated. Unusually heavy plumage weight probably reduced heat production in Tipplers.

The presence of ataxia did not measurably affect rate of heat production. The critical temperature for individuals with scraggly plumage was apparently the same (30° C.) as that for normal adult pigeons. In young Carneau pigeons the rate of heat production was as low at 25° as at 30° C.

Measurements on two congenitally blind pigeons studied in adult and senile states indicated a diminished adult rate (effect of relative inactivity?) of heat production, but a nearly normal rate in the senile state.

Several though not all hybrid types supply evidence that rate of heat production is an inherited trait. Insufficient numbers of F_1 and F_2 hybrids prevented the accumulation of information concerning the mode of inheritance of this trait. Heat production was studied on F_1 hybrids obtained from crossing a dove and a pigeon; dissimilar body size of parents and hybrids here prevents a satisfactory evaluation of relative heat production in the parental and hybrid types.

TABLE 14

Respiratory metabolism (calories per kilogram per hour) of ring doves of race 75 and of hybrids of races 75 and B

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
Race 75									
		Males				Females			
30	Spring	12	4.87	0.71	2	13	5.11*	0.72	3
	Summer	15	5.12	0.73	4	12	5.41*	0.70	3
	Autumn	7	5.08	0.73	2	14	5.45*	0.71	2
	Winter	14	4.90	0.73	7	14	5.14*	0.72	3
	Yr. av.	*48*	*4.99*	*0.73*	*15*	*53*	*5.28**	*0.71*	*11*
20	Spring	14	6.64	0.72	10	19	6.94*	0.73	9
	Summer	12	6.99	0.71	7	11	7.51*	0.73	3
	Autumn	23	7.08	0.72	10	23	7.62	0.72	11
	Winter	23	6.63	0.74	9	22	6.94*	0.70	7
	Yr. av.	*72*	*6.83*	*0.72*	*36*	*75*	*7.25**	*0.72*	*30*
15	Spring	6	8.23	0.71	2	5	8.57*	0.72	3
	Summer	7	7.96	0.74	2	8	7.94	0.71	2
	Autumn	5	8.85	0.72	2	8	8.61*	0.71	4
	Winter	9	7.13	0.73	3	12	8.14*	0.74	5
	Yr. av.	*27*	*8.04*	*0.73*	*9*	*33*	*8.31**	*0.72*	*14*
		Old birds (55+ months)							
30	Spring	4	4.71	....	..	1	4.79	....	..
	Summer	2	4.75	....	..	1	5.09	....	..
	Winter	2	4.81	....	..	..	....	....	..
20	Spring	2	6.91	0.70	2	2	6.80	....	..
	Summer	1	7.13	0.73	1	..	....	....	..
	Autumn	1	6.77	....	..	1	6.23	0.69	1
	Winter	2	6.87	0.69	2	1	7.09*	0.75	1
	Yr. av.	*6*	*6.92*	*0.71*	*5*	*4*	*(6.71)**	*0.72*	*2*

*Includes one or more measurements made on females within 50 hours of ovulation.

(*Continued on following page*)

TABLE 14—*Continued*

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
HYBRIDS, 75 × B									
		Males				Females			
30	Spring	6	4.65	0.78	2	7	5.12*	0.75	2
	Summer	6	4.58	0.75	4	7	4.90*	0.74	2
	Autumn	4	5.08	0.73	3	3	5.05	0.79	1
	Winter	5	4.66	0.75	4	5	4.76	0.70	3
	Yr. av.	_21_	_4.74_	_0.75_	_13_	_22_	_4.96*_	_0.75_	_8_
20	Spring	5	6.20	0.74	5	12	6.03*	0.73	6
	Summer	5	5.88	0.70	1	9	6.51*	0.71	3
	Autumn	8	6.46	0.72	4	10	6.78*	0.73	3
	Winter	10	6.18	0.73	5	17	6.24*	0.72	11
	Yr. av.	_28_	_6.18_	_0.72_	_15_	_48_	_6.39*_	_0.72_	_23_
15	Spring	2	6.61	0.71	1	1	6.55*	0.71	1
	Summer	1	8.22	0.70	1	1	7.05	0.70	1
	Autumn	5	7.87	0.73	3	9	7.70	0.72	5
	Winter	2	6.98	0.72	1	6	8.22*	0.72	5
	Yr. av.	_10_	_7.42_	_0.72_	_6_	_17_	_7.38*_	_0.71_	_12_
		Old birds (55+ months)							
30	Spring	..	....	....	..	1	4.34	....	..
	Summer	..	....	....	..	1	5.23*	0.74	1
	Autumn	1	4.74	0.72	1	..	....	....	..
	Winter	..	....	....	..	2	4.22	0.70	1
20	Spring	1	6.18	....	..	2	6.09*	0.74	2
	Summer	..	....	....	..	1	6.30	0.72	1
	Autumn	1	7.22	0.73	1	3	6.65	0.74	1
	Winter	..	....	....	..	1	6.12	....	..
	Yr. av.	..	....	....	..	_7_	_6.29_	_0.73_	_4_
15	Summer	..	....	....	..	1	7.07	0.68	1
	Winter	..	....	....	..	2	7.11	0.71	1

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 15

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF RING DOVES OF RACE B AND OF HYBRIDS OF RACES 36 AND B

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
				RACE B					
		Males				Females			
30	Spring	10	4.47	0.71	4	10	4.96*	0.70	5
	Summer	8	4.41	0.69	6	10	4.81*	0.71	7
	Autumn	10	5.15	0.73	7	7	5.15*	0.71	4
	Winter	5	4.09	0.72	4	8	4.85	0.71	3
	Yr. av.	*33*	*4.53*	*0.71*	*21*	*35*	*4.94**	*0.71*	*19*
20	Spring	17	5.75	0.72	13	17	5.88*	0.71	12
	Summer	14	6.02	0.71	10	17	6.18*	0.71	12
	Autumn	11	6.46	0.72	8	9	6.62*	0.70	4
	Winter	16	5.86	0.73	10	17	6.26	0.74	10
	Yr. av.	*58*	*6.02*	*0.72*	*41*	*60*	*6.23**	*0.72*	*38*
15	Spring	5	6.98	0.71	2	3	6.98*	0.72	1
	Summer	2	6.55	0.71	1	3	6.82*	0.66	1
	Autumn	9	7.44	0.71	6	8	7.49	0.74	3
	Winter	6	6.60	0.72	4	8	6.90*	0.72	5
	Yr. av.	*22*	*6.89*	*0.71*	*13*	*22*	*7.05**	*0.71*	*10*
				Old birds (55+ months)					
30	Spring	2	4.29	0.73	1	1	4.96	0.74	1
	Summer	1	4.27	0.76	1	1	5.25	0.76	1
	Winter	1	4.25	....	..	..	....	....	..
20	Spring	2	6.15	0.70	2	2	8.08	0.73	2
	Autumn	1	7.62	....	..	1	6.32	0.71	1
	Winter	1	6.48	....	..	1	6.50	....	..
				HYBRIDS, 36 × B					
30	Spring	7	5.19	0.71	2	7	4.78*	0.74	4
	Summer	6	4.82	0.74	2	10	5.15*	0.71	2
	Autumn	7	5.16	0.73	2	10	5.24	0.74	4
	Winter	1	5.15	....	..	4	4.38*	0.73	2
	Yr. av.	*21*	*5.08*	*0.73*	*6*	*31*	*4.89**	*0.73*	*12*
20	Spring	3	5.82	0.73	1	3	5.52	0.72	1
	Summer	6	6.31	0.71	2	5	5.99*	0.72	2
	Autumn	4	6.49	0.72	2	6	6.12	0.72	2
	Winter	5	5.87	0.70	2	8	5.58	0.72	6
	Yr. av.	*18*	*6.12*	*0.72*	*7*	*22*	*5.80**	*0.72*	*11*
15	Spring	2	7.22	0.69	1	2	7.27	0.79	1
	Autumn	..	....	....	..	1	6.25	....	..
	Winter	3	7.13	0.73	3	3	7.06	0.68	2
				Old birds (55+ months)					
20	Autumn	1	6.31	0.73	1				
15	Winter	1	6.69	....	.				

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 16

Respiratory metabolism (calories per kilogram per hour) of hybrids of ring dove races 62 and 75 and of races 72 and 75

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
	Hybrids, 62 × 75								
		Males				Females			
30	Spring	6	4.50	0.73	3	4	4.53*	0.70	2
	Summer	8	4.66	0.67	4	7	4.57*	0.69	4
	Autumn	1	4.56	0.74	1	2	5.19*	0.71	1
	Winter	5	4.52	0.76	5	4	4.55*	0.74	3
	Yr. av.	*20*	*4.56*	*0.73*	*13*	*17*	*4.71**	*0.71*	*10*
20	Spring	11	5.96	0.71	8	13	6.07*	0.72	8
	Summer	7	6.16	0.73	3	7	6.23*	0.69	2
	Autumn	2	6.24	0.74	2	3	6.80	0.72	1
	Winter	16	6.02	0.72	8	10	5.99*	0.73	5
	Yr. av.	*36*	*6.10*	*0.73*	*21*	*33*	*6.27**	*0.72*	*16*
15	Spring	3	7.22	0.72	1	3	7.05	....	..
	Summer	4	6.76	0.74	2	3	6.86*	0.74	1
	Autumn	7	7.46	0.72	4	6	7.70*	0.72	3
	Winter	7	6.86	0.72	5	6	7.36*	0.68	3
	Yr. av.	*21*	*7.07*	*0.73*	*12*	*18*	*7.24**	*0.71*	*7*
		Old birds (55+ months)							
20	Spring	2	5.75	0.76	2				
	Summer	1	5.74	0.68	1				
	Winter	1	5.46	0.72	1				
	Hybrids, 72 × 75								
30	Spring	10	4.51	0.72	4	4	5.06	0.76	1
	Summer	3	4.68	0.69	2	5	5.52	0.72	3
	Autumn	6	4.96	0.71	3	9	5.26*	0.72	5
	Winter	9	4.76	0.76	4	8	5.08	0.74	4
	Yr. av.	*28*	*4.73*	*0.72*	*13*	*26*	*5.23**	*0.74*	*13*
20	Spring	4	6.56	0.73	1	10	6.04*	0.72	3
	Summer	5	6.25	0.71	2	4	7.10*	0.74	2
	Autumn	9	6.61	0.74	3	9	7.01*	0.71	4
	Winter	10	6.65	0.71	3	13	6.36*	0.74	7
	Yr. av.	*28*	*6.52*	*0.72*	*9*	*36*	*6.63**	*0.73*	*16*
15	Spring	2	7.00	....	..	2	7.62*	....	..
	Summer	..	....	....	..	2	8.36	0.71	1
	Autumn	2	7.58	0.70	1	2	7.19	0.72	1
	Winter	3	7.47	0.72	1	3	6.73*	....	..
	Yr. av.	..	....	....	..	*9*	*7.48**	....	..
		Old birds (55+ months)							
30	Spring	3	4.60	0.71	1	..	....	....	..
	Autumn	3	4.90	0.72	3	1	4.48	....	..
20	Summer	1	7.53	0.68	1	..	....	....	..
	Autumn	..	....	....	..	1	5.76	....	..
	Winter	..	....	....	..	1	5.53	0.72	1
15	Winter	1	7.24	0.73	1	..	....	....	..

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 17

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF RING DOVES OF RACE 62 AND OF HYBRIDS OF RACES 11 AND 62

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		RACE 62							
		Males				Females			
30	Spring	11	4.06	0.71	6	7	4.62*	0.71	3
	Summer	11	4.40	0.73	8	10	4.50*	0.72	8
	Autumn	9	4.64	0.71	4	5	4.64	0.70	4
	Winter	5	3.98	0.71	1	4	4.21	0.74	1
	Yr. av.	*36*	*4.27*	*0.71*	*19*	*26*	*4.49**	*0.72*	*16*
20	Spring	18	5.83	0.71	3	12	5.77*	0.72	5
	Summer	13	5.69	0.71	5	8	5.92*	0.69	4
	Autumn	10	6.31	0.72	5	9	6.22	0.70	5
	Winter	17	5.84	0.71	7	13	5.71	0.72	6
	Yr. av.	*58*	*5.92*	*0.71*	*20*	*42*	*5.90**	*0.71*	*20*
15	Spring	7	6.75	0.72	2	9	6.91*	0.73	4
	Summer	6	7.28	0.72	2	2	7.10	0.68	1
	Autumn	6	7.36	0.71	2	5	7.48	0.72	3
	Winter	12	7.16	0.72	5	8	6.55*	0.72	5
	Yr. av.	*31*	*7.13*	*0.72*	*11*	*24*	*7.01**	*0.71*	*13*
		Old birds (55+ months)							
30	Spring	2	3.84	0.71	1				
	Summer	2	4.28	0.71	1				
	Autumn	1	4.28	....	..				
	Winter	1	3.29	0.76	1				
	Yr. av.	*6*	*3.92*	*0.73*	*3*				
20	Spring	2	5.73	0.69	1				
	Autumn	4	6.72	0.73	2				
	Winter	4	5.92	....	..				
15	Winter	1	7.46	....	..				
		HYBRIDS, 11 × 62							
30	Spring	4	4.83	0.73	2	6	4.80	0.72	4
	Summer	3	4.42	0.71	1	4	4.78*	0.70	3
	Autumn	4	4.83	0.75	1	5	5.23	0.70	2
	Winter	4	4.43	0.74	1	2	4.76	0.75	1
	Yr. av.	*15*	*4.63*	*0.73*	*5*	*17*	*4.89**	*0.72*	*10*
20	Spring	5	5.55	0.73	3	5	5.81*	0.71	3
	Summer	4	5.87	0.67	2	1	5.31	....	..
	Autumn	5	6.41	0.73	3	6	5.92	0.71	1
	Winter	3	5.53	0.70	1	4	5.64	0.72	2
	Yr. av.	*17*	*5.84*	*0.71*	*9*	*16*	*5.67**	*0.71*	*6*
15	Spring	4	5.94	0.73	3	3	6.71	0.71	2
	Summer	2	7.07	....	..	2	6.80*	0.67	1
	Autumn	3	6.84	0.70	1	1	6.19	0.72	1
	Winter	..	....	....	..	3	6.74	....	..
	Yr. av.	*9*	*6.62*	*0.72*	*4*	*9*	*6.61**	*0.70*	*4*
		Old bird (78 months)							
20	Winter	..	....	....	..	1	5.73		

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 18

Respiratory metabolism (calories per kilogram per hour) of hybrids of ring dove races B and 62 and of races 63 and 62

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
	Hybrids, B × 62								
		Males				Females			
30	Spring	5	4.60	0.73	3	6	5.07*	0.70	4
	Summer	5	4.29	0.72	3	6	4.91*	0.73	5
	Autumn	6	4.79	0.71	4	6	5.02	0.71	5
	Winter	5	4.59	0.72	3	8	4.54*	0.75	5
	Yr. av.	*21*	*4.57*	*0.72*	*13*	*26*	*4.89**	*0.72*	*19*
20	Spring	8	5.69	0.73	5	12	5.92*	0.71	3
	Summer	7	5.80	0.72	3	7	5.91*	0.69	3
	Autumn	12	6.48	0.70	8	12	6.50*	0.71	7
	Winter	11	6.44	0.71	5	16	6.40*	0.71	8
	Yr. av.	*38*	*6.10*	*0.72*	*21*	*47*	*6.18**	*0.71*	*21*
15	Spring	3	6.73	0.74	1	4	6.78	0.74	3
	Autumn	1	7.23	0.72	1	3	7.37*	0.73	2
	Winter	1	7.08	....	..	1	7.56	....	..
			Old birds (55+ months)						
30	Spring	2	3.99	0.73	2	2	5.24	0.73	2
	Summer	1	4.60	0.67	1	2	5.19*	0.74	2
	Autumn	2	4.31	0.72	2	2	4.88	0.72	2
	Winter	1	4.04	0.73	1	1	5.28*	0.73	1
	Yr. av.	*6*	*4.24*	*0.71*	*6*	*7*	*5.15**	*0.73*	*7*
20	Spring	4	6.15	0.72	2	2	5.69*	0.75	1
	Summer	1	6.94	0.72	1	1	7.19*	....	..
	Autumn	4	6.74	0.72	3	4	6.98	0.72	1
	Winter	3	6.53	0.73	2	2	6.22	....	..
	Yr. av.	*12*	*6.59*	*0.72*	*8*	*9*	*6.52**	....	..
15	Spring	1	8.79	0.72	1	1	7.22	....	..
	Winter	1	6.05	0.75	1	1	6.45	....	..
	Hybrids, 63 × 62								
30	Spring	11	3.89	0.73	7	4	4.36*	0.77	1
	Summer	9	4.19	0.72	4	10	4.77*	0.71	4
	Autumn	5	4.44	0.72	4	6	4.84	....	..
	Winter	6	4.33	0.71	4	5	4.62*	0.74	3
	Yr. av.	*31*	*4.21*	*0.72*	*19*	*25*	*4.65**	*0.74*	*8*
20	Spring	10	5.83	0.71	6	8	5.84*	0.70	5
	Summer	9	5.76	0.69	2	4	5.99*	0.72	2
	Autumn	5	5.83	0.71	4	8	6.53	0.69	5
	Winter	11	5.80	0.72	2	9	6.37	0.71	4
	Yr. av.	*35*	*5.81*	*0.71*	*14*	*29*	*6.18**	*0.71*	*16*
15	Spring	1	7.13	....	..	1	7.36	....	..
	Autumn	3	6.85	0.72	2	1	6.07	0.69	1
	Winter	3	6.09	0.73	2	3	6.79	0.73	2
	(Yr. av.)	*7*	*(6.69)*	....	..	*5*	*(6.74)*	....	..

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 19

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF HYBRIDS OF RING DOVE RACES B AND 72 AND OF RACES 36 AND 62

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
				HYBRIDS, B × 72					
		Males				Females			
30	Spring	4	4.63	0.72	1	4	5.05*	0.72	1
	Summer	1	4.74	0.68	1	5	5.03*	0.73	1
	Autumn	5	4.86	0.72	2	5	5.13	0.70	2
	Winter	4	4.81	0.72	2	5	4.92*	0.69	1
	Yr. av.	*14*	*4.76*	*0.71*	*6*	*19*	*5.03**	*0.71*	*5*
20	Spring	9	5.59	0.72	6	8	6.23	0.71	6
	Summer	7	6.35	0.71	5	7	6.00*	0.74	2
	Autumn	4	6.40	0.72	4	7	6.44*	0.71	7
	Winter	9	6.04	0.73	7	14	5.99*	0.72	9
	Yr. av.	*29*	*6.10*	*0.72*	*22*	*36*	*6.16**	*0.72*	*24*
15	Spring	1	7.84	0.71	1	3	7.57	0.72	3
	Summer	2	6.84	....	..	2	6.87*	....	..
	Autumn	6	7.59	0.73	4	7	7.59	0.71	5
	Winter	3	7.07	0.74	2	4	7.38*	0.73	2
	Yr. av.	*12*	*7.33*	*0.72*	*7*	*16*	*7.35**	*0.72*	*10*
				Old birds (55+ months)					
30	Spring	1	4.62	....	..	2	4.17*	0.72	2
	Summer	2	4.41	....	..	2	4.52	....	..
	Autumn	3	4.68	0.72	2	2	5.22	....	..
	Winter	..	....	....	..	1	4.37	0.70	1
	Yr. av.	..	....	....	..	*7*	*4.57**	....	..
20	Spring	2	5.44	0.75	2	3	5.70*	0.73	1
	Summer	1	6.51	....	..	2	5.19	0.71	1
	Autumn	2	6.78	0.74	2	1	5.93	0.96	1
	Winter	2	5.83	0.73	2	1	5.51	0.80	1
	Yr. av.	*7*	*6.14*	*0.74*	*6*	*7*	*5.58*	*0.80*	*4*
15	Autumn	1	6.95	0.74	1	..	....	....	..
				HYBRIDS, 36 × 62					
30	Spring	8	4.24	0.71	4	11	4.48*	0.69	3
	Summer	5	4.34	0.69	1	7	4.84*	0.72	3
	Autumn	2	4.90	....	..	3	4.89	0.69	1
	Winter	5	4.18	0.75	3	8	4.38	0.73	2
	Yr. av.	*20*	*4.42*	*0.72*	*8*	*29*	*4.65**	*0.71*	*9*
20	Spring	3	5.87	0.73	2	4	5.69*	0.71	4
	Summer	6	5.96	0.70	2	6	6.09*	0.68	2
	Autumn	9	6.15	0.70	4	10	6.65	0.70	2
	Winter	15	5.78	0.72	7	7	6.52*	0.73	3
	Yr. av.	*33*	*5.94*	*0.71*	*15*	*27*	*6.24**	*0.71*	*11*
15	Spring	4	6.95	....	..	5	6.62	0.71	2
	Summer	1	7.35	0.72	1	2	7.21	0.70	2
	Autumn	5	7.57	0.72	2	5	7.10	0.73	2
	Winter	7	6.83	0.72	2	8	7.44*	0.71	2
	Yr. av.	*17*	*7.18*	*(0.72)*	*5*	*20*	*7.09**	*0.71*	*8*

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 20

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF RING DOVES OF RACE G AND OF HYBRIDS OF RACES 72 AND 62

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
				RACE G					
		Males				Females			
30	Spring	3	3.70	0.73	1	3	4.14	0.78	1
	Autumn	4	4.64	0.73	2	4	4.54	0.77	2
	Winter	4	4.14	0.72	3	3	4.09	0.73	2
	Yr. av.	*11*	*(4.16)*	*0.73*	*6*	*10*	*(4.26)*	*0.76*	*5*
20	Spring	4	5.92	....	..	3	6.17*	0.73	1
	Autumn	5	6.69	0.73	2	3	6.31	....	..
	Winter	2	6.98	0.74	1	1	5.77*	....	..
	Yr. av.	*11*	*(6.53)*	*0.74*	*3*	*7*	*(6.08)**	*0.73*	*1*
15	Spring	1	6.26	0.71	1	1	7.48*	....	..
	Autumn	1	6.93	....	..	1	7.70*	....	..
	Winter	2	7.26	0.78	1	1	5.97	....	..
	Yr. av.	*4*	*(6.82)*	*0.75*	*2*	*3*	*(7.05)**	....	..
				HYBRIDS, 72 × 62					
30	Spring	4	4.32	0.73	3	9	4.45*	0.75	4
	Summer	10	4.45	0.71	5	6	4.84*	0.69	3
	Autumn	8	4.68	0.72	4	12	4.62*	0.71	12
	Winter	6	4.26	0.71	5	10	4.57*	0.73	4
	Yr. av.	*28*	*4.43*	*0.72*	*17*	*37*	*4.62**	*0.72*	*23*
20	Spring	15	6.04	0.73	4	12	5.91*	0.72	2
	Summer	14	6.46	0.69	10	14	6.16*	0.71	10
	Autumn	9	6.33	0.72	5	13	6.36*	0.71	7
	Winter	18	6.66	0.72	11	21	6.12*	0.71	11
	Yr. av.	*56*	*6.38*	*0.72*	*30*	*60*	*6.13**	*0.71*	*30*
15	Spring	3	6.76	0.71	3	3	6.62*	0.72	3
	Summer	3	7.59	0.69	2	2	7.97	0.72	2
	Autumn	4	7.92	0.73	2	5	7.18*	0.71	1
	Winter	13	7.45	0.72	7	10	6.95*	0.71	5
	Yr. av.	*23*	*7.43*	*0.71*	*14*	*20*	*7.18**	*0.72*	*11*
				Old birds (55+ months)					
30	Spring	1	3.91	0.70	1	..	....	....	..
	Summer	2	4.21	0.69	1	2	4.26	0.73	2
	Autumn	4	4.04	0.72	3	1	4.57	0.69	1
	Winter	2	3.94	0.68	1	1	4.48	0.70	1
	Yr. av.	*9*	*4.03*	*0.70*	*6*	..	....	....	..
20	Spring	3	6.36	0.75	1	1	5.59	0.72	1
	Summer	3	6.41	0.74	1	2	5.88*	0.71	2
	Autumn	3	6.64	0.69	1	1	5.58	....	..
	Winter	3	6.14	0.72	3	1	6.17	....	..
	Yr. av.	*12*	*6.39*	*0.73*	*6*	*5*	*5.81*	....	..
15	Spring	1	7.53	0.74	1	..	....	....	..
	Winter	2	7.05	0.72	2	..	....	....	..

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 21

Respiratory metabolism (calories per kilogram per hour) of ring doves of race OT

Temp. (°C.)	Season	No. of tests	Calories	R.Q. Value	R.Q. No.	No. of tests	Calories	R.Q. Value	R.Q. No.
			Males				Females		
30	Spring	13	3.94	0.75	8	18	4.51*	0.74	4
	Summer	8	4.33	0.74	4	17	4.68*	0.70	9
	Autumn	12	4.82	0.74	5	10	4.75*	0.73	8
	Winter	9	4.16	0.75	4	9	4.67*	0.74	4
	Yr. av.	*42*	*4.31*	*0.75*	*21*	*54*	*4.65**	*0.73*	*25*
20	Spring	14	5.74	0.73	8	14	5.75*	0.71	8
	Summer	17	6.03	0.72	7	8	5.90*	0.72	4
	Autumn	18	6.12	0.72	11	25	6.16*	0.71	14
	Winter	16	6.07	0.72	11	22	6.00*	0.73	15
	Yr. av.	*65*	*5.99*	*0.72*	*37*	*69*	*5.95**	*0.72*	*41*
15	Spring	4	6.93	0.73	4	5	7.12*	0.72	4
	Summer	5	7.06	0.71	3	9	7.12*	0.71	6
	Autumn	8	7.26	0.72	5	11	7.11*	0.73	8
	Winter	12	7.16	0.71	5	7	7.23	0.72	4
	Yr. av.	*29*	*7.10*	*0.72*	*17*	*32*	*7.15**	*0.72*	*22*
				Old birds (55+ months)					
30	Spring	..	....	....	..	4	4.54	0.72	3
	Summer	..	....	....	..	4	4.54*	0.65	1
	Autumn	..	....	....	..	3	4.68	0.67	3
	Winter	1	3.93	....	..	5	4.40	0.71	2
	Yr. av.	..	....	....	..	*16*	*4.54**	*0.69*	*9*
20	Spring	1	6.99	0.70	1	8	6.01*	0.73	4
	Summer	1	7.14	....	..	7	5.64	0.74	3
	Autumn	..	....	....	..	6	6.36*	0.71	5
	Winter	1	7.24	....	..	7	6.07	0.73	6
	Yr. av.	..	....	....	..	*28*	*6.02**	*0.73*	*18*
15	Autumn	1	8.93	0.73	1	3	7.30	0.73	3
	Winter	..	....	....	..	1	6.18	0.73	1
				Castrated bird					
20	Spring	2	6.15	0.73	1				
	Winter	1	6.26	....	..				
15	Spring	1	8.02	....	..				
	Winter	1	7.52	....	..				

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*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 22

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF RING DOVES OF RACE W

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Males				Females			
30....	Spring.....	3	4.84	0.73	2	6	4.86*	0.70	4
	Summer....	10	4.79	0.73	8	8	5.02*	0.72	6
	Autumn....	4	5.02	0.72	3	9	5.04*	0.70	4
	Winter.....	2	4.71	0.69	2	3	4.98	0.70	3
	Yr. av....	*19*	*4.84*	*0.72*	*15*	*26*	*4.98**	*0.71*	*17*
20....	Spring.....	11	6.21	0.72	6	11	6.71	0.73	5
	Summer....	9	6.66	0.73	6	10	6.58*	0.72	6
	Autumn....	10	6.98	0.72	8	11	6.74*	0.71	7
	Winter.....	8	6.04	0.70	4	10	6.16	0.70	3
	Yr. av....	*38*	*6.47*	*0.72*	*24*	*42*	*6.55**	*0.72*	*21*
15....	Spring.....	5	7.31	0.74	3	4	6.85	0.74	2
	Summer....	..	....	....	..	1	8.74	....	..
	Autumn....	6	7.44	0.73	5	8	7.39	0.73	5
	Winter.....	5	7.01	0.73	5	6	6.93	0.72	6
	Yr. av....	*16*	*7.25*	*0.73*	*13*	*19*	*7.48*	*0.73*	*13*
		Old birds (55+ months)							
30....	Spring.....	1	4.30	....	..	2	4.61*	....	..
	Summer....	1	4.83	0.70	1	..	....	....	..
	Autumn....	2	4.81	0.75	1	1	4.01	0.67	1
	Winter.....	1	4.13	....	..	1	5.01	....	..
	Yr. av....	*5*	*4.52*	*0.73*	*2*	..	....	....	..
20....	Spring.....	1	6.59	0.72	1	2	5.67	0.71	1
	Summer....	1	6.39	0.72	1	1	6.29	0.71	1
	Winter.....	2	5.92	0.71	1	1	5.90	0.71	1

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 23

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF RING DOVES OF RACE 36

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Adult males				Old males (55+ months)			
30	Spring	3	4.39	0.69	1	1	4.10	....	..
	Summer	2	4.36	....	..	1	4.60	....	..
	Autumn	4	4.58	0.70	2	2	4.41	0.68	1
	Winter	4	4.53	0.71	2	1	3.77	0.73	1
	Yr. av.	*13*	*4.47*	*0.70*	*5*	*5*	*4.22*	*0.71*	*2*
20	Spring	3	5.33	....	..	..	....	....	..
	Summer	2	5.71	....	..	3	5.33	....	..
	Autumn	4	6.51	0.71	1	3	6.84	0.71	1
	Winter	3	5.86	0.73	2	6	5.64	0.73	2
	Yr. av.	*12*	*5.85*	*0.72*	*3*	*12*	*(5.94)*	*0.72*	*3*
15	Spring	1	6.71	....	..	..	....	....	..
	Summer	..	....	....	..	1	7.14	....	..
	Autumn	2	6.79	0.70	1	1	8.00	....	..
	Winter	2	7.59	0.71	2	2	6.66	0.73	2

TABLE 24

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF RING DOVES OF RACE 63 AND OF HYBRIDS OF RACES 63 AND O (OR OT)

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
				RACE 63					
				Males				Females	
30	Spring.....	6	4.43	0.71	3	7	5.05*	0.73	2
	Summer....	10	4.62	0.71	5	9	5.20*	0.77	5
	Autumn....	5	4.56	....	..	7	5.16*	....	..
	Winter.....	7	4.94	0.74	3	7	4.81	0.74	7
	Yr. av....	*28*	*4.64*	*0.72*	*11*	*30*	*5.05**	*0.75*	*14*
20	Spring.....	13	6.20	0.71	7	21	6.46*	0.72	9
	Summer....	4	6.37	0.69	2	10	6.80*	0.74	4
	Autumn....	18	6.41	0.72	8	23	6.52*	0.71	12
	Winter.....	10	6.06	0.75	2	16	6.26*	0.73	3
	Yr. av....	*45*	*6.26*	*0.72*	*19*	*70*	*6.51**	*0.73*	*28*
15	Spring.....	3	7.32	0.69	1	8	7.51*	0.72	5
	Summer....	3	7.47	0.72	2	1	6.76	0.73	1
	Autumn....	4	7.27	0.70	1	4	8.46	....	..
	Winter.....	8	6.67	0.71	2	9	6.94*	0.74	7
	Yr. av....	*18*	*7.11*	*0.71*	*6*	*22*	*7.42**	*0.73*	*13*
				Old birds (55+ months)					
30	Spring.....	1	4.09	0.73	1				
20	Spring.....	3	6.14	0.70	2				
	Summer....	3	7.37	0.71	1				
	Autumn....	4	6.59	0.79	1				
	Winter.....	5	6.21	0.74	2				
	Yr. av....	*15*	*6.58*	*0.74*	*6*				
15	Spring.....	1	6.86	0.74	1				
	Autumn....	2	7.88	....	..				
	Winter.....	3	7.53	0.73	3				
				HYBRIDS, 63 × O (or OT)					
30	Spring.....	8	4.38	0.73	1	6	4.54	0.69	1
	Summer....	2	4.23	0.72	2	1	4.23	0.71	1
	Autumn....	4	4.59	0.74	1	3	5.14*	0.75	1
	Winter.....	2	4.17	....	..	2	4.46	....	..
	Yr. av....	*16*	*4.34*	*0.73*	*4*	*12*	*4.59**	*0.72*	*3*
20	Spring.....	1	5.83	....	..	3	6.18	0.72	2
	Summer....	3	6.49	....	..	4	6.15*	0.71	4
	Autumn....	4	6.80	0.72	1	3	7.15	0.71	2
	Winter.....	4	6.00	0.71	1	4	5.55	0.72	1
	Yr. av....	*12*	*6.28*	*0.72*	*2*	*14*	*6.26**	*0.72*	*9*
15	Spring.....	2	6.69	....	..	3	7.26*	0.72	2
	Autumn....	1	7.38	....	..	..	....	....	..
	Winter.....	1	6.59	....	..	1	6.42	....	..
				Old bird (55+ months)					
30	Spring.....	1	4.21	0.70	1				
	Autumn....	1	4.02	0.72	1				
	Winter.....	1	3.93	....	..				
20	Spring.....	1	6.49	....	..				

*Includes one or more measurements made on females within 50 hours of ovulation

TABLE 25

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF HYBRIDS OF RING DOVE RACES 63 AND 44 AND OF RACES N2 AND 63

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		HYBRIDS, 63 × 44							
		Males				Females			
30	Spring	8	4.13	0.73	5	5	4.52	0.71	3
	Summer	5	4.63	0.70	2	3	5.12	....	..
	Autumn	3	4.74	0.69	2	6	5.03*	0.70	3
	Winter	3	4.30	0.70	2	2	4.52	0.69	1
	Yr. av.	*19*	*4.45*	*0.71*	*11*	*16*	*4.79**	*0.70*	*7*
20	Spring	7	6.23	0.73	4	3	5.92*	0.73	3
	Summer	8	6.57	0.75	4	6	6.14*	0.70	4
	Autumn	9	6.47	0.72	6	7	6.08*	0.72	5
	Winter	7	6.35	0.72	7	7	6.04*	0.71	7
	Yr. av.	*31*	*6.41*	*0.73*	*21*	*23*	*6.04**	*0.72*	*19*
15	Spring	1	7.52	0.75	1	..	....	....	..
	Summer	2	7.09	0.71	2	3	7.01*	0.71	2
	Autumn	3	8.00	0.73	2	4	7.90	0.72	3
	Winter	3	7.66	0.73	2	3	7.08	....	..
	Yr. av.	*9*	*7.57*	*0.73*	*7*	*10*	*(7.33)**	*0.72*	*5*
		Old birds (55+ months)							
30	Spring	1	4.29	....	..	1	5.06	0.74	1
	Summer	1	5.19	....	..	..	....	....	..
	Autumn	1	4.96	....	..	..	....	....	..
	Winter	1	4.52	0.73	1	..	....	....	..
20	Spring	..	....	....	..	1	6.66	0.72	1
15	Spring	1	7.56	0.72	1	..	....	....	..
	Winter	..	....	....	..	1	8.67	0.71	1
		HYBRIDS, N2 × 63							
30	Spring	5	4.54	0.75	1	9	4.73	0.73	3
	Summer	4	4.87	0.70	1	5	5.31*	0.70	3
	Autumn	3	4.83	0.71	2	3	5.24	0.72	2
	Winter	3	4.54	0.72	2	3	4.95*	0.67	1
	Yr. av.	*15*	*4.69*	*0.72*	*6*	*20*	*5.06**	*0.71*	*9*
20	Spring	2	6.98	0.73	2	3	7.69*	0.69	1
	Summer	3	6.51	....	..	3	6.09	....	..
	Autumn	8	6.60	0.74	3	10	6.59*	0.74	6
	Winter	3	6.33	0.72	1	6	6.63*	0.70	4
	Yr. av.	*16*	*6.60*	*0.73*	*6*	*22*	*6.75**	*0.71*	*11*
15	Summer	1	7.34	....	..	1	7.53	....	..
	Autumn	2	7.97	....	..	4	8.67*	....	..
	Winter	1	6.43	0.71	1	1	7.80*	0.71	1

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 26

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF RING DOVES OF RACE N2 AND OF HYBRIDS OF RACES NE AND N2

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
				RACE N2					
			Males				Females		
30	....Spring.....	16	5.21	0.73	8	14	4.81*	0.70	7
	Summer....	16	5.18	0.71	6	13	5.17*	0.72	7
	Autumn....	11	5.24	0.70	4	8	5.33	0.71	3
	Winter.....	13	4.95	0.74	6	11	4.70*	0.72	5
	Yr. av....	*56*	*5.14*	*0.72*	*24*	*46*	*5.00**	*0.71*	*22*
20	....Spring.....	24	6.89	0.72	11	22	6.55*	0.72	12
	Summer....	14	7.36	0.70	5	16	6.50*	0.69	6
	Autumn....	14	7.10	0.72	3	19	6.96*	0.72	10
	Winter.....	10	6.85	0.72	2	13	6.54*	0.74	4
	Yr. av....	*62*	*7.05*	*0.72*	*21*	*70*	*6.64**	*0.72*	*32*
15	....Spring.....	4	7.88	0.72	3	10	7.33	0.73	4
	Summer....	3	8.91	0.75	3	6	8.14*	0.74	5
	Autumn....	7	7.99	0.73	4	10	8.04*	0.71	5
	Winter.....	8	7.65	0.73	4	10	7.34*	0.74	3
	Yr. av....	*22*	*8.11*	*0.73*	*14*	*36*	*7.71**	*0.73*	*17*
				Old female (55+ months)					
30	....Spring.....	..	....	....	..	1	4.79	0.75	1
	Summer....	..	....	....	..	1	4.96	0.70	1
20	....Spring.....	..	....	....	..	1	6.53	....	..
	Summer....	..	....	....	..	1	6.66*	....	..
	Autumn....	..	....	....	..	1	7.82	....	..
	Winter.....	..	....	....	..	1	6.81	....	..
	Yr. av....	..	....	....	..	*4*	*6.95*	....	..
15	....Winter.....	..	....	....	..	1	7.12	....	..
				HYBRIDS, NE × N2					
30	....Spring.....	3	4.79	....	..	4	5.11*	....	..
	Summer....	6	4.97	....	..	6	5.44*	0.73	4
	Autumn....	4	4.78	0.69	1	2	5.76	0.70	1
	Winter.....	1	4.62	....	..	2	6.15	0.72	2
	Yr. av....	*14*	*4.79*	*0.69*	*1*	*14*	*5.61**	*0.72*	*7*
20	....Spring.....	4	6.61	....	..	3	6.87*	....	..
	Summer....	3	7.31	0.69	2	2	7.31	0.67	1
	Autumn....	4	6.51	0.70	3	2	7.11	0.73	2
	Winter.....	1	6.81	....	..	3	6.80	0.75	1
	Yr. av....	*12*	*6.81*	....	..	*10*	*7.02**	*0.72*	*4*
15	....Spring.....	..	....	....	..	1	8.42	....	..
	Autumn....	4	8.16	....	..	3	7.90	0.69	1
	Winter.....	1	7.33	....	..	1	8.07*	....	..

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 27

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF HYBRIDS OF RING DOVE RACES N2 AND 62

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Males				Females			
30	Spring	9	4.28	0.73	3	11	4.67*	0.71	6
	Summer	12	4.72	0.74	6	8	4.85*	0.70	4
	Autumn	5	4.37	0.74	4	6	4.81*	0.71	4
	Winter	4	4.31	0.70	2	4	4.87	0.73	3
	Yr. av.	*30*	*4.42*	*0.73*	*15*	*29*	*4.80**	*0.71*	*17*
20	Spring	11	6.21	0.72	8	15	6.03*	0.70	9
	Summer	12	6.57	0.72	6	13	6.32*	0.72	7
	Autumn	6	6.47	0.73	3	9	6.41	0.72	7
	Winter	7	5.92	0.73	4	12	5.90*	0.72	7
	Yr. av.	*36*	*6.29*	*0.73*	*21*	*49*	*6.17**	*0.72*	*30*
15	Spring	4	6.73	0.69	1	7	7.05*	0.70	4
	Summer	2	6.94	....	..	2	6.46*	....	..
	Autumn	2	6.64	....	..	6	7.27	0.73	2
	Winter	3	6.21	0.68	1	4	6.97	0.70	1
	Yr. av.	*11*	*6.63*	....	..	*19*	*6.94**	*0.71*	*7*
				Old birds (55+ months)					
30	Spring	3	4.18	0.72	2	6	4.52*	0.74	1
	Summer	1	4.28	0.68	1	1	4.20	0.70	1
	Autumn	1	4.52	0.66	1	3	4.80	0.73	2
	Winter	2	4.42	0.77	2	4	4.68	0.73	1
	Yr. av.	*7*	*4.35*	*0.71*	*6*	*14*	*4.55**	*0.73*	*5*
20	Spring	4	5.79	0.74	3	3	5.71*	0.73	3
	Summer	1	6.48	0.73	1	1	6.06*	0.68	1
	Autumn	2	6.58	....	..	3	7.25	0.75	2
	Winter	2	5.41	....	..	3	5.66	0.75	1
	Yr. av.	*9*	*6.06*	....	..	*10*	*6.17**	*0.73*	*7*
15	Autumn	1	6.41	....	..	1	6.75	0.70	1

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 28

Respiratory metabolism (calories per kilogram per hour) of hybrids of ring dove races 44 and N2

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Males				Females			
30	Spring	5	4.49	0.73	3	9	5.44*	0.73	5
	Summer	11	5.19	0.73	3	10	5.53*	0.72	4
	Autumn	6	5.04	0.72	1	6	5.51	0.70	2
	Winter	8	4.89	0.80	1	8	5.44	0.78	2
	Yr. av.	*30*	*4.90*	*0.75*	*8*	*33*	*5.48**	*0.73*	*13*
20	Spring	16	6.32	0.73	9	13	7.28*	0.72	6
	Summer	5	6.43	0.72	3	13	7.16*	0.72	8
	Autumn	9	6.35	0.73	3	8	7.35*	0.71	4
	Winter	12	6.37	0.72	4	16	7.82*	0.73	5
	Yr. av.	*42*	*6.37*	*0.73*	*19*	*50*	*7.40**	*0.72*	*23*
15	Spring	4	7.17	0.73	1	2	6.58	0.72	1
	Summer	2	7.39	0.71	1	2	7.43	0.76	2
	Autumn	4	8.14	0.69	3	2	7.61	0.70	2
	Winter	4	6.78	0.71	2	8	8.20*	0.73	4
	Yr. av.	*14*	*7.37*	*0.71*	*7*	*14*	*7.45**	*0.73*	*9*
		Old birds (55+ months)							
30	Spring	1	4.57	....	..	2	5.12*	0.70	1
	Summer	3	4.66	0.69	2	4	5.66*	0.69	2
	Autumn	..	....	....	..	1	5.56*	....	..
	Winter	2	4.19	0.75	1	3	4.65	0.71	1
	Yr. av.	..	....	....	..	*10*	*5.25**	*0.70*	*4*
20	Spring	2	6.27	0.71	2	5	6.76*	0.73	3
	Summer	4	6.73	0.71	4	3	7.40*	0.73	2
	Autumn	1	6.80	0.75	1	3	8.18	0.72	2
	Winter	3	7.41	0.72	1	4	6.97*	0.72	3
	Yr. av.	*10*	*6.80*	*0.72*	*8*	*15*	*7.33**	*0.73*	*10*
15	Spring	..	....	....	..	2	7.34*	0.75	1

*Includes one or more measurements made on females within 50 hours of ovulation

TABLE 29

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF RING DOVES OF RACE 51. NORMAL BIRDS AND BIRDS SHOWING MYOCLONUS COMPLEXUS ARE LISTED SEPARATELY

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Normal adults							
		Males				Females			
30	Spring	12	4.74	0.73	5	17	5.14*	0.71	5
	Summer	15	4.69	0.74	5	14	5.11*	0.72	6
	Autumn	16	5.01	0.74	5	9	5.03	0.73	1
	Winter	10	4.71	0.70	5	15	4.94	0.73	8
	Yr. av.	*53*	*4.79*	*0.73*	*20*	*55*	*5.06**	*0.72*	*20*
20	Spring	18	5.90	0.74	7	19	6.23*	0.71	11
	Summer	19	6.34	0.72	8	14	6.38*	0.71	8
	Autumn	21	6.13	0.73	11	17	6.44	0.74	6
	Winter	21	5.92	0.72	11	22	6.27*	0.71	9
	Yr. av.	*79*	*6.07*	*0.73*	*37*	*72*	*6.33**	*0.72*	*34*
15	Spring	10	6.81	0.72	4	11	7.18*	0.71	6
	Summer	3	7.19	0.72	3	4	7.53	0.74	1
	Autumn	4	6.90	0.73	2	5	7.14	0.73	3
	Winter	22	6.69	0.72	14	14	7.16	0.74	6
	Yr. av.	*39*	*6.90*	*0.72*	*23*	*34*	*7.25**	*0.73*	*16*
		Myoclonic adults							
30	Spring	7	4.97	0.72	2	6	5.03*	0.71	3
	Summer	8	4.66	0.71	3	2	4.92	....	..
	Autumn	15	4.84	0.71	9	8	5.51	0.72	3
	Winter	7	4.66	0.71	3	7	5.10*	0.69	3
	Yr. av.	*37*	*4.78*	*0.71*	*17*	*23*	*5.14**	*0.71*	*9*
20	Spring	8	5.94	0.72	3	8	6.35	0.72	2
	Summer	15	6.10	0.72	7	4	6.58	0.75	2
	Autumn	10	6.16	0.72	6	9	6.65	0.73	5
	Winter	10	5.72	0.73	2	5	6.64	....	..
	Yr. av.	*43*	*5.98*	*0.72*	*18*	*26*	*6.56*	*0.73*	*9*
15	Spring	5	7.54	0.72	4	3	7.30*	0.75	1
	Summer	9	6.75	0.71	4	2	7.03*	....	..
	Autumn	5	6.86	0.73	3	1	8.54	....	..
	Winter	13	6.80	0.72	4	13	7.05*	0.73	6
	Yr. av.	*32*	*6.99*	*0.72*	*15*	*19*	*7.48**	*0.74*	*7*

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 30

Respiratory metabolism (calories per kilogram per hour) of hybrids of ring dove races 63 and 51

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Males				Females			
30	Spring	4	4.42	0.75	2	2	4.87	....	..
	Summer	5	4.75	0.74	1	3	4.93	....	..
	Autumn	5	5.03	0.73	1	5	5.20	0.71	1
	Winter	4	4.79	0.75	2	5	4.74*	0.72	3
	Yr. av.	*18*	*4.75*	*0.74*	*6*	*15*	*4.93**	....	..
20	Spring	11	5.93	0.72	4	7	5.77*	0.76	4
	Summer	4	5.63	0.72	3	4	6.19	0.71	1
	Autumn	5	6.02	0.74	2	3	6.48	0.72	1
	Winter	10	5.65	0.74	6	8	5.63*	0.75	5
	Yr. av.	*30*	*5.81*	*0.73*	*15*	*22*	*6.02**	*0.74*	*11*
15	Spring	2	7.57	....	..	2	7.20	0.73	1
	Summer	1	7.13	0.68	1	..	....	....	..
	Autumn	1	6.45	0.71	1	..	....	....	..
	Winter	3	6.49	0.73	3	3	6.64	0.75	3
	Yr. av.	*7*	*6.91*	*0.71*	*5*	..	....	....	..
		Old birds (55+ months)							
30	Spring	1	3.72	....	..				
	Autumn	1	4.61	....	..				
	Winter	1	3.91	....	..				
20	Spring	3	5.17	0.71	1				
	Summer	2	6.33	....	..				
	Autumn	2	5.84	....	..				
	Winter	2	5.30	0.73	2				
	Yr. av.	*9*	*5.66*	....	..				
15	Winter	1	6.21	....	..				

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 31

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF RING DOVES OF RACE 72

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
			Males				Females		
30	Spring	51	4.25	0.74	20	37	4.69*	0.72	20
	Summer	55	4.49	0.72	27	54	4.92*	0.71	20
	Autumn	53	4.78	0.72	21	43	4.98*	0.73	19
	Winter	53	4.25	0.75	24	39	4.63	0.74	17
	Yr. av.	*212*	*4.44*	*0.73*	*92*	*173*	*4.80**	*0.72*	*76*
20	Spring	59	5.96	0.72	23	59	5.96*	0.72	22
	Summer	56	6.42	0.72	19	51	6.29*	0.73	16
	Autumn	74	6.50	0.73	35	60	6.59*	0.72	27
	Winter	72	6.08	0.73	34	64	5.99*	0.72	37
	Yr. av.	*261*	*6.24*	*0.73*	*111*	*234*	*6.21**	*0.72*	*102*
15	Spring	18	7.36	0.71	4	13	6.97*	0.71	8
	Summer	4	7.98	0.70	1	4	7.19	0.70	1
	Autumn	13	7.81	0.73	3	12	8.10*	0.72	4
	Winter	31	7.23	0.74	11	27	7.05*	0.73	11
	Yr. av.	*66*	*7.60*	*0.72*	*19*	*56*	*7.33**	*0.72*	*24*
				Old birds (55+ months)					
30	Spring	8	4.45	0.77	2	4	4.51*	0.74	3
	Summer	6	4.54	0.72	4	2	4.92*	0.71	1
	Autumn	7	4.54	0.73	6	3	4.83	0.75	2
	Winter	6	4.34	0.71	3	4	4.62	0.75	2
	Yr. av.	*27*	*4.47*	*0.73*	*15*	*13*	*4.72**	*0.74*	*8*
20	Spring	5	5.90	0.71	3	..	....	....	..
	Summer	10	6.52	0.72	8	3	6.93*	0.71	1
	Autumn	6	6.67	0.74	2	2	6.41	0.73	1
	Winter	6	6.25	0.74	3	4	6.48	0.74	3
	Yr. av.	*27*	*6.33*	*0.73*	*16*	*9*	*(6.61)**	*0.73*	*5*
15	Spring	2	7.08	....	..	..	....	....	..
	Autumn	3	7.77	0.78	1	1	7.26*	0.74	1
	Winter	2	6.95	0.72	2	..	....	....	..

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 32

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF HYBRIDS OF RING DOVE RACES 72 AND 63

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Males				Females			
30	Spring	19	4.31	0.71	15	21	4.72*	0.73	12
	Summer	10	4.52	0.70	6	17	5.00*	0.71	9
	Autumn	16	4.56	0.73	10	24	5.18*	0.72	11
	Winter	17	4.41	0.74	8	29	4.92*	0.72	12
	Yr. av.	*62*	*4.45*	*0.72*	*39*	*91*	*4.95**	*0.72*	*44*
20	Spring	24	5.80	0.73	11	28	6.15*	0.72	15
	Summer	17	6.22	0.72	10	23	6.37*	0.72	10
	Autumn	20	6.61	0.72	8	34	6.55*	0.73	17
	Winter	17	5.84	0.73	8	26	6.04*	0.73	10
	Yr. av.	*78*	*6.12*	*0.73*	*37*	*111*	*6.28**	*0.73*	*52*
15	Spring	7	7.12	0.70	6	6	6.99*	0.71	3
	Summer	1	6.83	....	..	3	7.51*	....	..
	Autumn	8	7.93	0.72	4	22	8.01*	0.71	5
	Winter	7	7.10	0.73	3	18	7.23*	0.72	7
	Yr. av.	*23*	*7.24*	*0.72*	*13*	*49*	*7.44**	*0.71*	*15*
		Old birds (55+ months)							
30	Spring	3	4.30	0.71	3	6	4.39*	0.71	2
	Summer	1	4.01	0.71	1	1	4.55	0.75	1
	Autumn	1	4.71	0.72	1	3	4.83	0.72	2
	Winter	5	4.34	0.72	3	4	4.26*	0.75	3
	Yr. av.	*10*	*4.34*	*0.72*	*8*	*14*	*4.51**	*0.73*	*8*
20	Spring	3	6.23	0.73	3	7	6.30*	0.74	2
	Summer	2	6.37	0.73	2	5	6.28*	0.72	1
	Autumn	5	6.44	0.72	1	6	6.93	0.72	2
	Winter	3	6.53	0.75	2	7	5.83	0.73	4
	Yr. av.	*13*	*6.39*	*0.73*	*8*	*25*	*6.33**	*0.73*	*9*
15	Spring	1	6.03	0.71	1	1	7.70*	....	..
	Autumn	1	7.44	0.72	1	1	7.54*	....	..

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 33

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF HYBRIDS OF RING DOVE RACES 36 AND 72

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Males				Females			
30....	Spring.....	11	4.44	0.71	5	8	4.78*	0.70	4
	Summer....	16	4.58	0.71	11	15	4.91*	0.71	6
	Autumn....	20	4.77	0.71	10	12	5.12*	0.73	4
	Winter.....	13	4.46	0.77	3	11	4.59*	0.75	3
	Yr. av....	*60*	*4.56*	*0.73*	*29*	*46*	*4.85**	*0.72*	*17*
20....	Spring.....	20	5.84	0.71	10	16	5.90*	0.72	7
	Summer....	15	6.01	0.70	8	10	6.26*	0.74	5
	Autumn....	24	6.15	0.72	10	22	6.32*	0.72	11
	Winter.....	13	5.76	0.72	6	17	5.93*	0.74	5
	Yr. av....	*72*	*5.94*	*0.71*	*34*	*65*	*6.10**	*0.73*	*28*
15....	Spring.....	6	6.78	0.73	4	3	7.06	0.72	2
	Summer....	4	6.58	0.72	1	2	6.90*	0.72	1
	Autumn....	11	7.42	0.71	6	5	7.25	0.71	1
	Winter.....	7	6.54	0.72	5	7	6.74	0.71	5
	Yr. av....	*28*	*6.83*	*0.72*	*16*	*17*	*6.99**	*0.72*	*9*
		Old birds (55+ months)							
30....	Spring.....	..	....	....	..	2	4.45*	0.73	2
	Summer....	1	4.83	....	..	2	4.24	0.71	1
	Autumn....	..	....	....	..	1	5.23	0.69	1
20....	Spring.....	..	....	....	..	2	5.36	0.70	1
	Summer....	..	....	....	..	1	5.12	0.73	1
	Autumn....	1	6.03	....	..	..	....	....	..
	Winter.....	..	....	....	..	3	5.12	....	..
15....	Spring.....	..	....	....	..	2	6.33	....	..
	Autumn....	..	....	....	..	1	6.67	0.71	1

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 34

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF HYBRIDS OF RING DOVE RACES NA AND 72

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
			Males				Females		
30....	Spring.....	17	4.35	0.72	12	14	4.63*	0.72	6
	Summer....	10	4.80	0.70	3	10	4.82*	0.78	2
	Autumn....	14	4.64	0.72	7	12	4.54*	0.72	7
	Winter.....	8	4.60	0.74	5	8	4.62*	0.74	4
	Yr. av....	_49_	_4.60_	_0.72_	_27_	_44_	_4.65*_	_0.74_	_19_
20....	Spring.....	20	6.41	0.72	8	16	6.01*	0.71	3
	Summer....	14	6.78	0.71	7	11	6.76*	0.72	5
	Autumn....	21	6.68	0.72	9	21	6.24*	0.70	11
	Winter.....	18	6.24	0.72	9	17	6.18*	0.72	6
	Yr. av....	_73_	_6.53_	_0.72_	_33_	_65_	_6.30*_	_0.71_	_25_
15....	Spring.....	3	6.94	0.74	2	5	7.30	0.72	2
	Summer....	4	7.02	0.75	2	4	7.78	0.71	2
	Autumn....	13	7.45	0.73	8	7	8.18*	0.71	2
	Winter.....	11	7.36	0.74	5	12	7.07	0.75	3
	Yr. av....	_31_	_7.19_	_0.74_	_17_	_28_	_7.58_	_0.72_	_9_
				Old birds (55+ months)					
30....	Spring.....	..	....	....	..	2	4.52	0.72	1
	Summer....	1	4.85	....	..	1	4.22*	0.72	1
	Autumn....	..	....	....	..	2	5.02	0.69	1
20....	Spring.....	..	....	....	..	1	6.02	....	..
	Summer....	..	....	....	..	2	6.57	0.73	1
	Autumn....	..	....	....	..	1	6.08	0.72	1
	Winter.....	..	....	....	..	2	6.20	0.74	2
	Yr. av....	..	....	....	..	_6_	_6.22_	_0.73_	_4_

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 35

Respiratory metabolism (calories per kilogram per hour) of hybrids of ring dove races 72 and OT (or O)

Temp (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
			Males				Females		
30	Spring	19	4.25	0.72	6	17	4.67*	0.74	5
	Summer	9	4.44	0.68	3	11	4.66*	0.72	4
	Autumn	16	4.63	0.70	8	13	4.64*	0.72	8
	Winter	7	4.25	0.75	2	13	4.70*	0.73	12
	Yr. av.	*51*	*4.39*	*0.71*	*19*	*54*	*4.67**	*0.73*	*29*
20	Spring	22	6.22	0.71	12	22	5.87*	0.72	12
	Summer	12	6.20	0.73	5	6	5.89	0.75	1
	Autumn	20	6.35	0.72	12	14	6.41	0.72	8
	Winter	23	5.87	0.73	15	15	5.82*	0.74	9
	Yr. av.	*77*	*6.21*	*0.72*	*44*	*57*	*6.00**	*0.73*	*30*
15	Spring	5	7.49	0.72	3	5	6.92	0.71	5
	Summer	5	7.25	0.71	1	5	6.96*	0.65	2
	Autumn	10	7.42	0.73	4	6	6.90	0.72	4
	Winter	5	7.15	0.71	3	4	6.93*	0.71	1
	Yr. av.	*25*	*7.33*	*0.72*	*11*	*20*	*6.93**	*0.70*	*12*
				Old birds (55+ months)					
30	Spring	5	3.82	0.71	1				
	Summer	5	4.28	0.72	2				
	Autumn	3	4.36	....	..				
	Winter	3	4.32	0.71	1				
	Yr. av.	*16*	*4.20*	*0.71*	*4*				
20	Spring	7	5.69	0.75	2				
	Summer	3	6.09	0.70	1				
	Autumn	4	6.08	0.73	2				
	Winter	3	6.25	0.75	1				
	Yr. av.	*17*	*6.03*	*0.73*	*6*				
15	Autumn	1	8.03	0.73	1				
	Winter	1	6.60	0.74	1				

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 36

Respiratory metabolism (calories per kilogram per hour) of ring doves of race 67 and of hybrids of races 67 and 72

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of test	Calories	R.Q.	
				Value	No.			Value	No.
				Race 67					
		Males				Females			
30....	Spring.....	6	4.17	0.72	3	6	4.60*	0.72	3
	Summer....	10	4.55	0.70	4	7	4.75	0.78	2
	Autumn....	5	4.58	0.73	3	4	4.78	0.70	4
	Winter.....	8	4.18	0.79	5	7	4.38*	0.76	5
	Yr. av....	*29*	*4.37*	*0.74*	*15*	*24*	*4.63**	*0.74*	*14*
20....	Spring.....	19	6.12	0.72	11	13	5.95	0.75	6
	Summer....	8	6.63	0.74	5	4	6.14*	0.71	3
	Autumn....	16	6.14	0.72	8	9	6.01	0.74	4
	Winter.....	22	6.13	0.74	13	12	5.71*	0.74	6
	Yr. av....	*65*	*6.25*	*0.73*	*37*	*38*	*5.95**	*0.74*	*19*
15....	Spring.....	5	6.84	0.75	4	4	6.91*	0.71	1
	Summer....	..	....	....	..	1	7.10	....	..
	Autumn....	9	7.38	0.72	7	3	7.40	0.72	2
	Winter.....	8	6.81	0.72	5	6	6.58	0.70	3
	Yr. av....	*22*	*(7.01)*	*0.73*	*16*	*14*	*7.00**	*0.71*	*6*
		Old birds (55+ months)							
30....	Summer....	2	4.13	....	..	..	....	....	..
	Winter.....	2	4.19	....	..	1	4.38	0.75	1
20....	Spring.....	2	5.79	....	..	1	6.84*	....	..
	Autumn....	1	6.12	0.70	1	..	....	....	..
	Winter.....	..	....	....	..	1	5.71	....	..

*Includes one or more measurements made on females within 50 hours of ovulation.

(*Continued on following page*)

TABLE 36—*Continued*

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
				HYBRIDS, 67 × 72					
				Males				Females	
30	Spring	2	4.16	0.77	2	2	4.22	0.72	2
	Summer	5	4.79	0.74	5	5	4.70*	0.72	5
	Autumn	5	4.83	0.74	4	5	4.55	0.73	4
	Winter	6	4.12	0.74	3	6	4.28	0.72	4
	Yr. av.	*18*	*4.48*	*0.75*	*14*	*18*	*4.44**	*0.72*	*15*
20	Spring	3	5.77	0.68	1	4	5.49	0.71	1
	Summer	3	5.76	0.76	1	3	5.83*	0.69	1
	Autumn	9	6.19	0.71	6	9	5.96*	0.70	7
	Winter	5	5.49	0.72	3	5	5.29	0.73	3
	Yr. av.	*20*	*5.80*	*0.72*	*11*	*21*	*5.64**	*0.71*	*12*
15	Spring	3	7.13	0.73	2	3	7.08*	0.72	1
	Autumn	1	7.25	0.74	1	1	6.47	0.73	1
	Winter	3	7.00	0.72	1	3	7.18*	0.75	2
				Old birds (55+ months)					
			(One dove only)				(One dove only)		
30	Spring	1	3.83	0.74	1	1	4.29*	0.72	1
	Winter	2	4.40	0.77	2	2	4.54*	0.73	2
20	Spring	1	5.56	0.73	1	1	5.35	....	..
	Summer	1	5.93	0.75	1	1	5.78	0.70	1
	Autumn	1	6.00	0.70	1	1	5.78	....	..
	Winter	1	5.40	....	..	1	5.61	....	..
	Yr. av.	*4*	*5.72*	....	..	*4*	*5.63*	....	..

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 37

Respiratory metabolism (calories per kilogram per hour) of ring doves of race NA

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Males				Females			
30	Spring	14	4.57	0.72	8	15	4.96*	0.72	6
	Summer	11	4.65	0.71	3	17	4.78*	0.75	5
	Autumn	7	4.70	....	..	9	4.62	0.74	2
	Winter	6	4.49	0.70	2	11	4.73*	0.73	5
	Yr. av.	*38*	*4.60*	*0.71*	*13*	*52*	*4.77**	*0.74*	*18*
20	Spring	18	6.52	0.72	7	23	6.32*	0.71	11
	Summer	12	6.80	0.73	4	17	6.82*	0.72	5
	Autumn	9	6.95	0.72	6	13	6.95*	0.72	7
	Winter	9	6.30	0.73	3	13	6.36*	0.72	4
	Yr. av.	*48*	*6.64*	*0.73*	*20*	*66*	*6.61**	*0.72*	*27*
15	Spring	6	7.71	0.71	2	6	7.41*	0.70	3
	Summer	4	7.97	0.72	2	4	7.68	0.68	2
	Autumn	7	8.57	0.70	2	8	8.39*	0.70	3
	Winter	7	8.01	0.72	2	6	7.65*	0.68	1
	Yr. av.	*24*	*8.06*	*0.71*	*8*	*24*	*7.78**	*0.69*	*9*
		Bird without gonads							
30	Spring	1	4.10	....	..				
	Summer	1	4.53	....	..				
20	Spring	3	5.99†	....	..				
	Autumn	1	6.17	....	..				
		Old birds (55+ months)							
30	Spring	1	5.01	....	..	2	4.52*	0.72	1
	Summer	1	4.21	....	..	1	4.28	0.73	1
	Autumn	2	4.93	0.74	1	1	4.87	0.72	1
	Winter	2	4.17	0.75	1	1	4.19	0.69	1
	Yr. av.	*6*	*4.58*	*0.75*	*2*	*5*	*4.46**	*0.72*	*4*
20	Spring	2	6.53	....	..	..	....	....	..
	Summer	3	6.42	0.75	3	3	6.54*	0.74	1
	Autumn	2	6.29	....	..	1	6.11	....	..
15	Winter	1	7.26	0.72	1	..	....	....	..

*Includes one or more measurements made on females within 50 hours of ovulation.

†The temperature used was 22°.

TABLE 38

Respiratory metabolism (calories per kilogram per hour) of hybrids of ring dove races 65 and 163

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Males				Females			
30	Spring	13	4.19	0.72	7	13	4.73*	0.75	4
	Summer	9	4.60	0.69	2	7	5.40	0.68	2
	Autumn	7	4.77	0.75	5	9	4.63	0.74	4
	Winter	11	4.35	0.72	6	9	4.55	0.75	5
	Yr. av.	*40*	*4.48*	*0.72*	*20*	*38*	*4.83**	*0.73*	*15*
20	Spring	16	5.93	0.72	5	18	6.20*	0.71	5
	Summer	13	6.31	0.72	7	13	6.50*	0.75	7
	Autumn	11	6.57	0.73	5	13	6.52*	0.71	4
	Winter	18	6.20	0.72	13	20	6.02*	0.71	14
	Yr. av.	*58*	*6.25*	*0.72*	*30*	*64*	*6.31**	*0.72*	*30*
15	Spring	4	6.80	....	..	5	6.57	0.72	2
	Summer	..	....	....	..	1	7.07*	....	..
	Autumn	4	6.72	0.72	3	5	7.70	0.71	4
	Winter	5	6.55	0.73	3	5	6.55*	0.73	3
	Yr. av.	..	....	....	..	*16*	*6.98**	*0.72*	*9*
				Old birds (55+ months)					
30	Spring	2	3.91	0.76	1	2	4.45*	0.74	2
	Autumn	1	4.98	....	..	..	....	....	..
	Winter	2	4.17	0.70	1	1	4.03	....	..
20	Spring	2	5.27	0.75	2	1	5.03	0.74	1
	Autumn	..	....	....	..	1	6.32	....	..
	Winter	1	4.98	0.82	1	1	6.56	....	..

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 39

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF MISCELLANEOUS RING DOVE RACES. (COMBINED DATA FROM RACES K, 44, NE, 6, 29, 163, 65, AND 78.)

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Males				Females			
30	Spring	8	4.37	0.69	4	6	4.64	0.74	3
	Summer	10	4.75	0.71	4	11	5.14*	0.71	8
	Autumn	4	4.97	....	..	5	5.05	0.69	1
	Winter	2	3.98	0.74	1	1	4.27	....	..
	Yr. av.	*24*	*4.52*	*0.71*	*9*	*23*	*4.78**	*0.71*	*12*
20	Spring	6	6.16	0.70	1	6	6.46	0.72	3
	Summer	4	6.11	0.73	1	3	6.14*	....	..
	Autumn	12	5.98	0.72	6	13	6.43	0.72	4
	Winter	11	6.01	0.72	4	7	5.91*	0.72	2
	Yr. av.	*33*	*6.07*	*0.72*	*12*	*29*	*6.24**	*0.72*	*9*
15	Spring	2	7.08	0.73	2	..	....	....	..
	Summer	2	7.18	....	..	1	7.06	....	..
	Autumn	3	7.79	0.72	1	2	7.79*	....	..
	Winter	10	7.24	0.72	1	3	6.54*	0.71	1
	Yr. av.	*17*	*7.32*	*0.72*	*4*	*6*	*7.13**	*0.71*	*1*
		Old birds (55+ months)							
30	Spring	3	4.05	0.75	3	..	....	....	..
	Summer	2	4.23	0.72	2	1	4.77	....	..
	Autumn	2	4.23	0.71	1	..	....	....	..
	Winter	4	4.44	0.74	1	..	....	....	..
	Yr. av.	*11*	*4.24*	*0.73*	*7*	..	....	....	..
20	Spring	6	6.15	0.73	3	..	....	....	..
	Summer	6	6.43	0.71	4	..	....	....	..
	Autumn	4	6.28	0.74	2	1	6.46	....	..
	Winter	6	6.47	0.74	2	2	6.74	....	..
	Yr. av.	*22*	*6.33*	*0.73*	*11*	..	....	....	..
15	Summer	1	8.09	0.80	1	..	....	....	..
	Autumn	1	7.63	....	..	..	....	....	..
	Winter	2	7.65	....	..	1	6.32	....	..
	Yr. av.	*4*	*7.79*	*0.80*	*1*	..	....	....	..

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 40

Respiratory metabolism (calories per kilogram per hour) of several miscellaneous ring dove hybrids

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Males				Females			
30	Spring	38	4.77	0.72	12	33	4.93*	0.71	13
	Summer	33	4.75	0.70	17	33	5.08*	0.70	16
	Autumn	21	4.90	0.70	8	16	5.24*	0.71	5
	Winter	23	4.50	0.72	9	19	4.92	0.72	8
	Yr. av.	*115*	*4.73*	*0.71*	*46*	*101*	*5.04**	*0.71*	*42*
20	Spring	27	6.20	0.72	19	34	6.02*	0.72	16
	Summer	33	6.31	0.73	18	28	6.19*	0.73	13
	Autumn	41	6.29	0.72	20	41	6.45*	0.72	15
	Winter	24	5.98	0.74	10	20	6.02*	0.73	9
	Yr. av.	*125*	*6.20*	*0.73*	*67*	*123*	*6.17**	*0.73*	*53*
15	Spring	7	7.33	0.72	2	5	7.13	0.73	2
	Summer	9	7.00	0.69	7	9	6.79*	0.71	8
	Autumn	15	7.19	0.72	5	14	7.51*	0.72	5
	Winter	18	6.86	0.71	8	13	7.36*	0.73	10
	Yr. av.	*49*	*7.10*	*0.71*	*22*	*41*	*7.20**	*0.72*	*25*
		Old birds (55+ months)							
30	Spring	2	3.81	0.77	1	..	....	....	..
	Summer	1	4.17	0.75	1	1	4.94	....	..
	Autumn	1	4.37	0.72	1	..	....	....	..
	Winter	3	4.75	0.72	2	..	....	....	..
	Yr. av.	*7*	*4.28*	*0.74*	*5*	..	....	....	..
20	Spring	5	5.79	0.71	1	1	6.07*	....	..
	Summer	4	6.45	....	..	..	....	....	..
	Autumn	2	6.10	0.68	1	..	....	....	..
	Winter	3	6.10	0.75	2	1	5.47	....	..
	Yr. av.	*14*	*6.11*	*0.71*	*4*	..	....	....	..
15	Autumn	2	7.44	0.71	2	1	7.70	0.68	1
	Winter	1	5.37	0.73	1	1	8.37	0.73	1

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 41

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF HYBRIDS FROM A PIGEON (RACE T) AND A RING DOVE (RACE 78)

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Adult males				Young males (2–4.5 months)			
30	Spring	4	4.73	0.76	2	..	....	....	..
	Winter	3	5.03	0.73	1	1	5.37	0.72	1
20	Spring	8	5.36	0.73	5	..	....	....	..
	Summer	6	5.39	0.72	4	..	....	....	..
	Autumn	8	5.66	0.74	6	3	6.51	0.73	2
	Winter	14	5.53	0.74	9	..	....	....	..
	Yr. av.	*36*	*5.49*	*0.73*	*24*	..	....	....	..
15	Autumn	1	6.94	....	..	..	....	....	..
	Winter	4	6.16	0.73	2	..	....	....	..

TABLE 42

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF ALL FEMALE RING DOVES OF RACE 72 MEASURED EITHER NEAR OVULATION OR AT NONOVULATION STAGES

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Nonovulation				At or near ovulation			
30	Spring	23	4.60	0.74	11	14	4.82	0.71	9
	Summer	44	4.92	0.71	17	10	4.89	0.70	3
	Autumn	41	4.99	0.73	19	2	4.57	0.70	1
	Winter	39	4.63	0.74	17	..	....	....	..
	Yr. av.	*147*	*4.79*	*0.73*	*64*	*26*	*(4.76)*	*0.70*	*13*
20	Spring	52	5.93	0.72	18	7	6.19	0.72	4
	Summer	43	6.32	0.73	14	8	6.12	0.74	2
	Autumn	58	6.57	0.72	27	2	6.89	....	..
	Winter	57	5.95	0.72	34	7	6.37	0.71	3
	Yr. av.	*210*	*6.19*	*0.72*	*93*	*24*	*6.39*	*0.72*	*9*
15	Spring	8	6.91	0.71	4	5	7.08	0.71	4
	Summer	4	7.19	0.70	1	..	....	....	..
	Autumn	11	8.09	0.72	4	1	8.27	....	..
	Winter	26	7.02	0.73	11	1	7.91	....	..
	Yr. av.	*49*	*7.30*	*0.71*	*20*	*7*	*(7.76)*	....	..
		Old birds (55+ months)							
30	Spring	3	4.41	0.72	2	1	4.79	0.79	1
	Summer	1	4.50	....	..	1	5.35	0.71	1
	Autumn	3	4.83	0.75	2	..	....	....	..
	Winter	4	4.62	0.75	2	..	....	....	..
	Yr. av.	*11*	*4.59*	*0.74*	*6*	..	....	....	..
20	Summer	2	7.21	0.71	1	1	6.38	....	..
	Autumn	2	6.41	0.73	1	..	....	....	..
	Winter	4	6.48	0.74	3	..	....	....	..
15	Autumn	..	....	....	..	1	7.26	0.74	1

TABLE 43

A comparison of heat production (calories per kilogram per hour) in females measured at the same season both at ovulation (within 50 hours) and at nonovulation stages. Data are for doves of race 72, for all other dove races, and for pigeons. For each "near ovulation" value obtained from race 72, the average nonovulation value obtained for the race at that season was made the basis for calculating the effect of this reproductive stage on metabolism. Signs (+ or −) indicate increase or decrease from nonovulation values.

Doves or pigeons	30°		20°		15°	
	No. of tests	Change (%) (+ or −)	No. of tests	Change (%) (+ or −)	No. of tests	Change (%) (+ or −)
Doves*	41	+1.04	97	+1.31	12	−1.50
Race 72	28	+2.55	25	+2.12	9	+6.07
All doves	69	+1.65	122	+1.48	21	+1.74
Pigeons	5	−1.72	35	−0.87	3	+9.02
Totals and averages	74	+1.44	157	+0.96	24	+1.90

*All races except race 72.

TABLE 44

YEARLY AVERAGE HEAT PRODUCTION (CALORIES PER KILOGRAM PER HOUR) AT 20° C. OF RACES AND HYBRIDS OF DOVES AND PIGEONS (SEXES COMBINED)

RING DOVES				PIGEONS			
Race	Calories	Hybrid	Calories	Race	Calories	Hybrid	Calories
75	7.04	NE × N2	6.92	SA-R (scr.)	7.16	M × 299	4.89*
		44 × N2	6.89				
N2	6.85	N2 × 63	6.68	Magpie	4.97	Misc.	4.76
		72 × 75	6.58				
NA	6.63	NA × 72	6.42	SA-R (atax.)	4.71	M × T	4.64
		75 × B	6.29				
W	6.51	65 × 163	6.28	SA-R (nor.)	4.66	R × M	4.51
		W × N2	6.27				
NE	6.40	63 × OT	6.27	SA-E (nor.)	4.64	T × SA-E	4.48
		72 × 62	6.26				
63	6.39	N2 × OT	6.24*	Homer	4.48	T × R	4.46
		N2 × 62	6.23				
72	6.23	63 × 44	6.23	Tippler	4.45	T × 267	4.45
		72 × 63	6.20				
51	6.20	62 × 75	6.19	267	4.45	H × 267	4.44
		Misc.	6.19				
Misc.	6.16	B × 62	6.14	299	4.31*	H × T	4.42
		B × 72	6.13				
B	6.13	72 × OT	6.11	Runt	4.24	SA-E × 267	4.41
		11 × 72	6.09*				
67	6.10	36 × 62	6.09	White King	4.09*	299 × R	4.40
		36 × 72	6.02				
OT	5.97	63 × 62	6.00	Homer C.	4.06	R × H	4.24
		36 × B	5.96				
62	5.91	63 × 51	5.92	Carneau	3.97	R × HC	4.22
		36 × N2	5.82				
36	5.85*†	72 × NE	5.78			R × SA-E	4.08
		11 × 62	5.76				
		67 × 72	5.72			C × HC	4.00*

*This value is for three seasons only.

†In race 36 only males were measured.

TABLE 45

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF TIPPLER PIGEONS

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
				Normal adults					
			Males				Females		
30	Spring	20	3.79	0.74	8	17	4.36*	0.73	9
	Summer	18	4.02	0.72	10	16	4.42*	0.73	6
	Autumn	19	4.36	0.73	8	20	4.40*	0.75	9
	Winter	14	3.87	0.76	6	14	4.22*	0.73	6
	Yr. av.	*71*	*4.01*	*0.74*	*32*	*67*	*4.35**	*0.74*	*30*
25	Spring	11	3.98	0.74	5	..	....	....	..
	Summer	4	4.21	0.70	2	4	4.54†	....	..
20	Spring	21	4.06	0.73	10	27	4.48*	0.72	12
	Summer	20	4.41	0.73	10	17	4.38*	0.72	8
	Autumn	20	4.70	0.74	6	20	4.82*	0.73	7
	Winter	19	4.19	0.74	5	20	4.54*	0.73	4
	Yr. av.	*80*	*4.34*	*0.74*	*31*	*84*	*4.56**	*0.73*	*31*
15	Spring	13	4.45	0.75	7	13	4.97*	0.73	5
	Summer	14	5.20	0.72	8	19	5.32*	0.73	9
	Autumn	11	4.94	0.72	6	10	4.99*	0.75	4
	Winter	21	4.69	0.73	9	21	4.81*	0.73	9
	Yr. av.	*59*	*4.82*	*0.73*	*30*	*63*	*5.02*	*0.74*	*27*
				Young birds (2–4.5 months)					
30	Spring	4	5.24	0.74	1	10	4.83	0.75	6
	Summer	4	4.73	0.74	1	5	4.85	0.73	3
	Autumn	1	5.20	....	..	1	5.27	....	..
20	Spring	10	5.18	0.72	6	14	5.14	0.75	5
	Summer	43	5.07	0.73	22	19	5.30	0.73	8
	Autumn	21	4.99	0.74	11	19	5.23	0.72	6
	Winter	12	4.97	0.73	8	10	5.24	0.75	4
	Yr. av.	*86*	*5.05*	*0.73*	*47*	*62*	*5.22*	*0.74*	*23*
				Castrated adults					
30	Summer	..	....	....	..	1	3.70	....	..
	Autumn	3	4.13	0.77	1	1	3.89	0.77	1
20	Spring	8	4.11	0.73	6	2	4.28	....	..
	Summer	7	4.45	0.74	4	2	4.55	0.73	1
	Autumn	4	4.81	0.75	1	2	4.90	0.76	1
	Winter	6	4.73	0.71	3	2	4.80	0.80	1
	Yr. av.	*25*	*4.53*	*0.73*	*14*	*8*	*4.63*	*0.76*	*3*
15	Autumn	4	4.97	0.75	1	1	5.61	0.72	1
				Old birds (60+ months)					
30	Spring	2	3.38	....	..	..	....	....	..
	Summer	1	3.28	0.76	1	..	....	....	..
	Autumn	1	3.33	....	..	1	4.47	....	..
	Winter	1	3.45	....	..	..	....	....	..
20	Spring	3	3.75	0.73	2	1	4.24	0.73	1
	Summer	2	3.71	0.71	1	1	4.74	0.73	1

*Includes one or more measurements made on females within 50 hours of ovulation.

†This group was measured at 28.1° C.

TABLE 46

Respiratory metabolism (calories per kilogram per hour) of pigeons of race SA-R. This race is composed of normal birds and of two mutational types. All adults, 4.5–60 months old.

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Normals							
		Males				Females			
30	Spring	13†	3.74	0.75	7	9	4.02*	0.77	5
	Summer	9†	3.84	....	..	6	4.14	0.70	1
	Autumn	10	4.31	0.73	3	6	4.04	0.73	2
	Winter	9	3.86	0.76	2	4	4.15*	0.80	1
	Yr. av.	*41*	*3.93*	*0.75*	*12*	*25*	*4.09**	*0.75*	*9*
25	Spring	3	3.76	0.77	1	..	....	....	..
	Summer	1	4.14	....	..	1	3.94	....	..
20	Spring	22†	4.37	0.71	9	14	4.71*	0.73	4
	Summer	14†	4.56	0.72	7	8	5.02*	0.73	2
	Autumn	16†	4.79	0.74	4	10	4.59*	0.75	2
	Winter	31†	4.40	0.72	11	15	4.84*	0.72	7
	Yr. av.	*83*	*4.53*	*0.72*	*31*	*47*	*4.79**	*0.73*	*15*
15	Spring	8†	5.24	0.75	4	6	5.07	0.74	4
	Summer	3	5.40	0.76	1	2	5.19	0.74	1
	Autumn	10	4.83	0.73	4	7	5.08	0.74	3
	Winter	17†	4.68	0.73	5	12	5.00	0.76	3
	Yr. av.	*38*	*5.04*	*0.74*	*14*	*27*	*5.09*	*0.74*	*11*
		Scragglies							
30	Spring	2†	4.74	0.75	2	3	4.65	0.75	1
	Summer	2	5.05	0.74	2	7	5.10	0.72	4
	Autumn	5†	5.10	0.77	3	1	5.09	0.73	1
	Winter	4	4.53	0.75	3	5	4.60	0.77	4
	Yr. av.	*13*	*4.86*	*0.75*	*10*	*16*	*4.86*	*0.74*	*10*
25	Summer	..	....	....	..	2	5.33	....	..
	Winter	2	7.12	0.74	2	..	....	....	..
20	Spring	6†	7.23	0.73	5	10	7.16*	0.74	4
	Summer	7	7.28	0.72	6	6	8.14	0.73	5
	Autumn	2†	6.61	0.75	1	7	7.21	0.75	3
	Winter	11	6.64	0.75	10	10	7.00*	0.73	5
	Yr. av.	*26*	*6.94*	*0.74*	*22*	*33*	*7.38**	*0.74*	*17*
15	Spring	5†	8.91	0.72	4	4	8.01*	0.73	3
	Summer	1	8.42	0.75	1	2	7.82	0.73	2
	Autumn	2	7.97	0.72	2	4	9.29	0.74	2
	Winter	10	7.70	0.73	6	9	8.16	0.75	3
	Yr. av.	*18*	*8.25*	*0.73*	*13*	*19*	*8.32**	*0.74*	*10*

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*Includes one or more measurements made on females within 50 hours of ovulation.

†Omitted from these numbers are measurements made on one bird (normal) which had smallest thyroids, and on one (scraggly) which was almost naked (see table 47).

(*Continued on following page*)

TABLE 46—*Continued*

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Ataxics							
		Males				Females			
30	Spring	9	3.86	0.76	3	6	4.24*	0.78	3
	Summer	9	4.01	0.72	4	7	4.14	0.73	3
	Autumn	6	4.21	0.75	2	2	3.91	....	..
	Winter	8	3.79	0.71	3	2	4.03	0.86	1
	Yr. av.	*32*	*3.97*	*0.73*	*12*	*17*	*4.08**	*0.79*	*7*
25	Summer	4	4.15	0.79	2	1	4.96	....	..
	Autumn	2	4.62	....	..	..	....	....	..
20	Spring	18	4.55	0.73	8	11	4.90	0.69	2
	Summer	12	4.68	0.72	6	8	4.92*	0.73	3
	Autumn	12	4.46	0.75	7	3	4.78	0.75	3
	Winter	15	4.35	0.75	7	8	5.00*	0.71	3
	Yr. av.	*57*	*4.51*	*0.74*	*28*	*30*	*4.90**	*0.72*	*11*
15	Spring	7	5.05	0.74	4	3	5.21	0.73	1
	Summer	2	4.83	0.71	1	2	5.88*	....	..
	Autumn	7	5.03	0.70	2	2	4.80	....	..
	Winter	10	4.43	0.74	7	5	5.15*	0.73	2
	Yr. av.	*26*	*4.84*	*0.72*	*14*	*12*	*5.28**	*0.73*	*3*

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 47

INDIVIDUAL RECORDS OF RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF TWO ABNORMAL MALE PIGEONS OF RACE SA-R

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Normal type, with smallest thyroids				Scraggly type, almost naked			
30	Spring	1	3.32	0.87	1	1	4.99	....	..
	Summer	2	3.36	....	..	..	....	....	..
	Autumn	..	....	....	..	1	5.58	0.75	1
25	Spring	3	3.89	....	..	..	....	....	..
	Summer	1	3.28	....	..	..	....	....	..
20	Spring	4	3.79	0.75	2	1	8.67	....	..
	Summer	1	3.96	....	..	..	....	....	..
	Autumn	2	4.57	....	..	1	10.41	0.73	1
	Winter	1	3.76	....	..	..	....	....	..
15	Spring	1	4.25	0.72	1	1	10.72	....	..
	Winter	1	3.53	0.74	1	..	....	....	..

TABLE 48

Respiratory metabolism (calories per kilogram per hour) of young (2–4.5 months) and old (60.0+ months) birds of a pigeon race, SA-R, containing two abnormal types

Temp. (° C.)	Season	No. of tests	Age (mos.)	Calories	R.Q.		No. of tests	Age (mos.)	Calories	R.Q.	
					Value	No.				Value	No.
					Normal						
			Young males					Young females			
20	Spring	1	4.1	4.79	....	.	.	....	....	....	.
	Autumn	1	3.9	4.81	....	.	1	4.5	4.58	....	.
					Ataxics						
30	Spring	.	....	....	....	.	1	2.9	4.18	....	.
	Summer	3	3.4	4.65	0.75	1	.	....	....	....	.
20	Spring	.	....	....	....	.	1	3.8	5.31*	....	.
	Autumn	1	4.4	4.79*	....	.	1	4.5	5.02	....	.
					Scragglies						
0	Spring	1	3.4	5.39	0.76	1	1	3.6	7.08	....	.
	Summer	.	....	....	....	.	1	2.9	5.34	....	.
	Autumn	1	3.2	6.82	0.75	1	2	3.0	5.83	0.71	1
20	Spring	.	....	....	....	.	2	2.7	7.46*	0.73	2
	Autumn	2	4.2	7.38	0.74	2	1	4.1	6.50	0.75	1
15	Winter	.	....	....	....	.	1	4.5	8.27	0.78	1
			Old *normal* males					Old *ataxic* males			
30	Spring	2	86.0	4.01	0.77	1	3	89.2	3.59	0.77	1
	Summer	1	84.5	3.93	....	.	.	....	....	....	.
	Autumn	1	64.4	4.61	0.76	1	1	68.9	3.86	....	.
	Winter	2	70.9	4.17	0.80	1	.	....	....	....	.
25	Spring	1	71.0	4.18	....	.	.	....	....	....	.
	Summer	2	69.4	4.26	0.74	1	1	77.9	3.91	....	.
	Autumn	1	75.9	4.23	....	.	.	....	....	....	.
	Winter	1	80.2	4.06	....	.	.	....	....	....	.
20	Spring	2	75.3	4.27	0.76	1	3	73.7	4.20	0.74	3
	Summer	1	74.7	4.56	0.75	1	6	79.2	4.43	0.74	4
	Autumn	.	....	....	....	.	4	73.1	4.58	0.73	3
	Winter	4	69.1	4.37	0.76	3	4	71.3	4.35	0.75	2

*The temperature used was 21° C.

TABLE 49

Data concerning zone of thermal neutrality in "scraggly" pigeons

Temp. (°C.)	No. of tests	Calories per kg. per hr.	R.Q.		No. of tests	Calories per kg. per hr.	R.Q.	
			Value	No.			Value	No.
		Males				Females		
33	2	5.46	....	. .	2	5.34	....	. .
30	6	4.79	0.75	5	12	4.85	0.76	8
28	1	4.73	0.73	1	3	5.28	0.74	3

TABLE 50

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF PIGEONS OF RACE SA-E AND OF HYBRIDS FROM TIPPLER × SA-E

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
	RACE SA-E								
		Males				Females			
30	Spring	8	3.62	0.78	4	11	4.14	0.78	4
	Summer	4	4.16	0.75	2	2	4.46	0.72	2
	Autumn	1	4.33	....	..	1	4.13	....	..
	Winter	2	3.92	0.81	2	1	4.39	....	..
	Yr. av.	*15*	*4.01*	*0.78*	*8*	*15*	*4.28*	*0.75*	*6*
20	Spring	6	4.30	0.73	2	7	4.77	0.71	2
	Summer	5	4.37	0.70	3	2	5.23*	0.73	1
	Autumn	17	4.73	0.74	6	9	4.94*	0.75	3
	Winter	7	4.32	0.72	3	4	4.45	0.71	3
	Yr. av.	*35*	*4.43*	*0.72*	*14*	*22*	*4.85*	*0.73*	*9*
15	Spring	2	5.33	....	..	3	4.30	0.75	1
	Summer	1	6.26	....	..	..	....	....	..
	Autumn	1	4.51	0.71	1	..	....	....	..
	Winter	7	4.63	0.75	5	4	4.97	0.74	3
	Yr. av.	*11*	*5.18*	*0.73*	*6*	*7*	*(4.64)*	*0.75*	*4*
				Old birds (60+ months)					
30	Summer	3	4.07	0.70	1				
	Autumn	2	4.26	0.73	1				
25	Autumn	1	4.34	....	..				
20	Spring	2	5.01†	....	..				
	Summer	1	5.55	....	..				
	Winter	3	4.69	0.77	1				
15	Spring	1	5.30	....	..				
	Autumn	1	5.63	....	..				
	Winter	2	5.06	....	..				

*Includes one or more measurements made on females within 50 hours of ovulation.
†The temperature used was 21° C.

(*Continued on following page*)

TABLE 50—*Continued*

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
HYBRIDS, TIPPLER × SA-E									
		Males				Females			
30	Spring	4	3.88	0.75	1	5	4.12*	0.80	2
	Summer	3	4.27	0.77	2	3	4.18	0.74	1
	Autumn	2	4.38	....	..	2	5.07	....	..
	Winter	1	3.98	....	..	1	4.32	....	..
	Yr. av.	*10*	*4.13*	....	..	*11*	*4.42*	....	..
20	Spring	21	4.23	0.76	8	15	4.52*	0.72	7
	Summer	4	3.97	0.78	1	9	4.75*	0.72	5
	Autumn	14	4.72	0.74	5	12	4.71*	0.74	4
	Winter	9	4.31	0.75	2	17	4.61*	0.72	6
	Yr. av.	*48*	*4.31*	*0.76*	*16*	*53*	*4.65**	*0.73*	*22*
15	Spring	11	4.63	0.74	4	8	4.72*	0.73	2
	Autumn	1	5.04	....	..	2	5.45	....	..
	Winter	..	....	....	..	5	4.62*	0.73	3
		Old birds (60+ months)							
30	Autumn	2	4.58	0.69	2				
20	Spring	2	4.11	0.83	1				
	Summer	4	4.52	0.67	2				
	Autumn	2	4.76	0.73	2				
	Winter	5	4.04	0.74	3				
	Yr. av.	*13*	*4.36*	*0.74*	*8*				

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 51

Respiratory metabolism (calories per kilogram per hour) of pigeon hybrids, Runt × race SA-E and races SA-E × 267

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
	Hybrids, Runt × SA-E								
		Males				Females			
30	Spring	4	3.64	0.72	1	5	3.79	0.75	3
	Summer	12	3.70	0.71	4	10	4.23*	0.72	6
	Autumn	7	4.17	0.77	3	5	4.51	0.78	2
	Winter	1	3.29	0.76	1	2	3.72	0.77	2
	Yr. av.	*24*	*3.70*	*0.74*	*9*	*22*	*4.06*	*0.76*	*13*
25	Spring	4	3.80	0.78	2	..	....	....	..
20	Spring	19	3.82	0.75	9	19	4.03*	0.75	13
	Summer	6	3.71	0.74	4	5	3.93	0.72	5
	Autumn	11	4.34	0.76	6	18	4.68*	0.73	6
	Winter	23	4.00	0.74	12	22	4.09*	0.74	15
	Yr. av.	*59*	*3.97*	*0.75*	*31*	*64*	*4.18*	*0.74*	*39*
15	Spring	2	4.23	0.73	1	5	4.12*	0.74	3
	Autumn	3	4.62	0.73	2	4	5.23	0.75	1
	Winter	7	4.30	0.75	6	10	4.46*	0.73	6
	Hybrids, SA-E × 267								
30	Spring	4	4.05	....	..	1	4.08	....	..
	Summer	2	4.19	0.71	1	2	4.17	....	..
	Autumn	1	3.97	0.75	1	1	4.57	0.72	1
20	Spring	8	3.80	0.76	2	4	4.58	0.75	1
	Summer	4	4.22	0.72	1	4	4.69*	....	..
	Autumn	6	4.45	0.72	3	7	4.69	0.72	3
	Winter	4	4.30	0.77	2	4	4.51	0.78	3
	Yr. av.	*22*	*4.19*	*0.74*	*8*	*19*	*4.62**	*0.75*	*7*
15	Spring	4	4.61	0.72	2	2	5.17	....	..
	Summer	1	5.98	0.72	1	1	6.91*	0.73	1
	Autumn	2	5.23	....	..	2	5.52*	....	..
	Winter	2	4.48	0.76	2	2	4.83	0.75	2
	Yr. av.	*9*	*5.07*	*0.73*	*5*	*7*	*5.61**	....	..
				Young birds (2–4.5 months)					
30	Spring	2	5.28	0.72	1	..	...	....	..
				Old birds (60+ months)					
30	Spring	7	3.48	0.80	1	..	....	....	..
	Summer	5	3.62	0.70	4	..	....	....	..
	Winter	5	3.53	0.77	2	..	....	....	..
20	Spring	6	3.88	0.76	2	..	....	....	..
	Summer	10	3.92	0.77	4	..	...		
	Autumn	1	3.89	0.74	1	1	5.25	0.71	1
	Winter	6	4.19	0.75	2	..	...	...	
	Yr. av.	*23*	*3.97*	*0.76*	*9*	..	..		

*Includes one or more measurements made on females within 50 hours of ovulation

TABLE 52

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF PIGEON HYBRIDS, TIPPLER × RACE 267, INCLUDING SEPARATE VALUES OBTAINED FOR A CONGENITALLY BLIND FEMALE

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.		No. of tests	Calo-ries	R.Q.		Per cent differ-ence from normal
				Value	No.			Value	No.			Value	No.	
		Males				Normal females				Blind female				
30	Spring	10	3.78	0.71	6	7	4.24*	0.75	2	1	3.82	....	..	−10
	Summer	1	3.69	0.75	1	5	4.22*	0.69	2	2	3.96	....	..	− 6
	Autumn	7	4.06	0.71	1	4	4.22	0.69	1	5	4.40	....	..	+ 4
	Winter	2	3.82	0.75	1	3	4.15*	0.76	2	2	4.00	....	..	− 3
	Yr. av.	*21*	*3.85*	*0.73*	*9*	*19*	*4.21**	*0.74*	*7*	*9*	*4.04*	....	..	*− 4*
25	Spring	..	....	....	..	..	....	....	..	2	4.22	....	..	....
	Summer	1	4.36	0.75	1	..	....	....	..	1	4.10	....	..	....
20	Spring	30	3.97	0.73	15	37	4.33*	0.72	16	3	4.12	0.71	1	− 5
	Summer	13	4.65	0.70	9	19	4.70*	0.71	7	2	4.13	....	..	−12
	Autumn	33	4.56	0.73	14	33	4.82*	0.72	12	4	4.74	0.65	1	− 2
	Winter	33	4.18	0.73	11	36	4.40*	0.74	20	4	4.25	....	..	− 3
	Yr. av.	*109*	*4.34*	*0.72*	*49*	*125*	*4.56**	*0.72*	*55*	*13*	*4.31*	....	..	*− 6*
15	Spring	6	4.38	0.72	3	6	4.67*	0.72	3	2	4.25	0.68	1	− 9
	Autumn	1	5.27	0.75	1	1	4.35*	0.84	1	1	5.46	0.77	1	+25
	Winter	7	4.31	0.73	3	8	4.85*	0.75	3	2	4.42	0.70	1	− 9
						Old birds (60 + months								
30	Spring	1	3.53	....	..	1	3.77	0.74	1	1	3.35	0.69	1	−11
	Summer	1	3.89	....	..	..	....	....	..	1	4.40	....	..	....
20	Spring	2	4.03	0.78	1	2	4.15*	....	..	2	3.99*	0.90	1	− 4
	Summer	2	4.48	0.73	1	1	4.07	....	..	1	4.70	0.68	1	+16
	Autumn	..	....	....	..	3	4.74	0.74	2	..	....	....	..	....
	Winter	..	....	....	..	1	3.81	0.75	1	..	....	....	..	....

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 53

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF MAGPIE PIGEONS, INCLUDING SEPARATE VALUES OBTAINED FOR A CONGENITALLY BLIND MALE

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.		Per cent difference from normal	No. of tests	Calories	R.Q.	
				Value	No.			Value	No.				Value	No.
		Normal males				Blind male					Females			
30	Spring	3	4.26	....	..	2	3.28	....	..	−23	2	4.50*	....	..
	Summer	3	3.92	0.70	1	1	3.68	....	..	− 6	1	4.20	....	..
	Autumn	2	4.44	....	..	4	4.12	....	..	− 7	2	4.50	....	..
	Winter	..	....	....	..	1	3.69	....	..	....	..	....	....	..
25	Spring	..	....	....	..	1	3.68	0.80	1	....	..	....	....	..
	Summer	..	....	....	..	2	3.72	0.83	1	....	..	....	....	..
20	Spring	14	4.76	0.77	3	2	3.96	....	..	−17	11	5.08*	0.75	4
	Summer	5	4.95	0.69	2	1	4.07	....	..	−18	4	4.98	0.68	2
	Autumn	12	5.33	0.74	5	2	4.93	....	..	− 8	6	5.48	0.73	3
	Winter	11	4.52	0.74	7	3	3.60	0.74	2	−20	8	4.61	0.73	5
	Yr. av.	*42*	*4.89*	*0.74*	*17*	*8*	*4.14*	....	..	*−15*	*29*	*5.04**	*0.72*	*14*
15	Spring	3	5.46	0.73	1	2	4.65	0.74	1	−15	2	6.10*	0.71	2
	Summer	1	6.58	....	..	..	....	....	..	..	2	6.15	....	..
	Autumn	7	5.53	0.73	2	1	5.67	....	..	+ 2	5	6.47	....	..
	Winter	6	5.14	0.79	1	2	4.11	0.77	1	−20	2	5.47*	0.78	1
	Yr. av.	*17*	*5.68*	*0.75*	*4*	..	....	....	..	....	*11*	*6.05**	....	..
						Old birds (60 + months)								
30	Spring	7	3.72	0.71	4	..	....	....	..	....				
	Summer	4	3.50	0.70	2	3	3.85	....	..	+10				
	Autumn	3	3.34	0.78	1	1	3.85	....	..	+15				
	Winter	4	3.56	0.71	2	1	3.22	....	..	−10				
20	Spring	10	4.70	0.74	4	3	4.15	....	..	−12				
	Summer	3	4.92	0.71	1	2	4.38	0.69	1	−11				
	Autumn	4	4.46	0.75	2	2	5.28	0.71	2	+18				
	Winter	..	....	....	..	1	4.19	....	..	....				

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 54

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF PIGEON HYBRIDS, HOMER × TIPPLER AND TIPPLER × RUNT

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
	HYBRIDS, HOMER × TIPPLER								
		Males				Females			
30	Spring	4	3.97	....	..	4	3.85*	0.73	1
	Summer	6	3.87	0.70	1	4	4.03*	0.74	1
	Autumn	11	4.27	0.72	3	3	4.11	0.73	2
	Winter	1	4.46	0.73	1	1	5.28*	0.75	1
	Yr. av.	*22*	*4.14*	*0.72*	*5*	*12*	*4.32**	*0.74*	*5*
20	Spring	12	4.13	0.73	4	10	4.67*	0.71	4
	Summer	4	4.38	....	..	4	4.42*	....	..
	Autumn	8	4.22	0.73	4	5	5.14*	0.73	2
	Winter	9	4.08	0.75	5	7	4.35*	0.72	3
	Yr. av.	*33*	*4.20*	*0.74*	*13*	*26*	*4.64**	*0.72*	*9*
15	Spring	3	4.52	0.72	1	3	5.31*	0.73	2
	Autumn	11	4.58	0.73	7	4	5.03	0.79	1
	Winter	1	5.04	....	..	1	4.79	....	..
		Old birds (60+ months)							
30	Spring	2	3.39	....	..				
	Summer	1	3.11	....	..				
	Autumn	1	3.62	....	..				
	Winter	1	3.49	....	..				
	Yr. av.	*5*	*3.40*	....	..				
20	Spring	1	3.42	....	..				
	Summer	2	3.85	....	..				
	HYBRIDS, TIPPLER × RUNT								
30	Summer	7	3.88	0.67	3	5	4.07*	0.74	2
	Autumn	3	4.08	....	..	3	4.46	....	..
25	Spring	1	3.65	0.73	1	..	....	....	..
20	Spring	3	4.48	0.69	1	5	4.82	0.72	1
	Summer	5	4.25	0.73	3	3	4.64*	0.74	2
	Autumn	8	4.49	0.70	5	9	4.71*	0.70	7
	Winter	8	4.09	0.72	2	10	4.19*	0.74	6
	Yr. av.	*24*	*4.33*	*0.71*	*11*	*27*	*4.59**	*0.73*	*16*
15	Summer	2	4.77	0.73	1	2	5.07*	0.73	1

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 55

Respiratory metabolism (calories per kilogram per hour) of pigeon hybrids, Runt × Magpie and Magpie × Tippler

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
Hybrids, Runt × Magpie									
		Males				Females			
30	Spring	1	3.70	0.73	1	5	3.75	0.72	1
	Summer	5	3.31	0.69	3	2	4.09	....	..
	Autumn	11	3.68	0.73	6	3	3.83*	0.77	2
	Winter	..	....	....	..	1	4.34	0.81	1
20	Spring	8	4.71†	0.72	8	7	4.84†	0.73	5
	Summer	1	4.18	0.69	1	1	4.78*	....	..
	Autumn	7	4.41	0.72	4	3	5.04*†	0.74	3
	Winter	7	4.04	0.74	5	5	4.06	0.76	2
	Yr. av.	*23*	*4.34*	*0.72*	*18*	*16*	*4.68**	*0.74*	*10*
15	Spring	2	4.92‡	0.75	1	1	6.21	0.70	1
	Autumn	2	4.85‡	0.71	1	2	5.53‡	0.73	1
	Winter	3	4.40	0.70	2	3	6.00*	0.72	1
		Young birds (2–4.5 months)							
30	Autumn	1	5.38	0.74	1	1	4.64	0.75	1
Hybrids, Magpie × Tippler									
30	Spring	2	4.24	0.76	1	..	....	....	..
	Summer	2	4.56	....	..	..	....	....	..
	Autumn	6	3.80	0.72	3	..	....	....	..
	Winter	3	3.82	0.78	1	..	....	....	..
	Yr. av.	*13*	*4.10*	*0.75*	*5*	..	....	....	..
25	Summer	1	4.22	....	..	..	....	....	..
	Autumn	2	3.82	....	..	..	....	....	..
20	Spring	9	4.33	0.73	1	12	4.38*	0.71	4
	Summer	7	4.43	0.72	1	8	4.90*	0.71	4
	Autumn	22	4.79	0.72	9	18	5.00*	0.71	10
	Winter	8	4.85	0.78	1	9	4.48*	0.73	2
	Yr. av.	*46*	*4.60*	*0.74*	*12*	*47*	*4.67**	*0.72*	*20*
15	Spring	4	5.21	0.77	1	8	4.99	0.75	5
	Summer	1	6.94‡	....	..	2	5.97*	....	..
	Autumn	2	5.46	....	..	2	5.17	....	..
	Winter	4	5.11	0.76	2	2	5.09*	0.70	1
	Yr. av.	*11*	*5.68*	....	..	*14*	*5.31*	....	..
		Old birds (60+ months)							
30	Spring	2	3.86	....	..	..	....	....	..
	Summer	2	3.60	....	..	..	....	....	..
	Autumn	3	3.44	0.75	1	..	....	....	..
	Winter	1	3.42	....	..	..	....	....	..
	Yr. av.	*8*	*3.58*	....	..	..	....	....	..
25	Spring	..	....	....	..	1	4.71		..
20	Spring	2	3.94	0.73	..	..	....		..
	Summer	1	4.07						..

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*Includes one or more measurements made on females within 50 hours of ovulation.

†The temperature used was 21°.

‡The temperature used was 16°

TABLE 56

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF PIGEONS OF RACE 299 AND OF HYBRIDS OF MAGPIE × 299

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
				RACE 299					
		Males				Females			
30	Spring	1	3.49	0.80	1	2	4.22*	....	..
	Summer	2	3.69	....	..	..	....	....	..
	Autumn	2	4.09	....	..	..	....	....	..
25	Autumn	1	3.94	0.77	1	..	....	....	..
20	Spring	6	3.94	0.76	2	1	4.87*	....	..
	Autumn	1	4.75	0.77	1	1	4.41	0.72	1
	Winter	3	3.94	0.75	2	1	3.96	0.73	1
15	Autumn	1	3.98	....	..	..	....	....	..
	Winter	4	4.57	0.72	3	1	4.66	....	..
				Old birds (60+ months)					
33	Winter	1	3.49	0.75	1	..	....	....	..
30	Autumn	1	4.18	0.80	1	..	....	....	..
20	Spring	..	....	....	..	1	3.71	....	..
	Autumn	1	4.82	....	..	..	....	....	..
	Winter	2	4.12	0.75	1	1	3.61	0.81	1
15	Winter	1	4.18	0.72	1	..	....	....	..
				HYBRIDS, MAGPIE × 299					
30	Spring	3	3.95	0.73	2	5	4.25	0.74	4
	Summer	1	4.14	0.69	1	2	4.55	0.73	1
	Winter	1	4.47	....	..	2	4.42	....	..
20	Spring	2	4.71	0.71	1	3	5.53*	0.70	2
	Summer	2	4.54	0.74	1	2	4.63	0.72	1
	Autumn	3	4.58	0.74	1	4	5.82*	0.74	2
	Winter	..	....	....	..	3	4.66	....	..
15	Winter	2	4.60	....	..	..	....	....	..

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 57

Respiratory metabolism (calories per kilogram per hour) of Runt pigeons and of hybrids of race 299 × Runt

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
				Runt					
		Males				Females			
30	Spring	14	3.44	0.77	8	9	3.67*	0.74	6
	Summer	8	3.41	0.77	3	8	3.70	0.76	3
	Autumn	7	4.07	0.74	5	6	3.78*	0.74	4
	Winter	2	3.23	....	..	2	3.19	0.82	1
	Yr. av.	*31*	*3.54*	*0.76*	*16*	*25*	*3.59**	*0.77*	*14*
20	Spring	17	3.92	0.76	11	14	4.32*	0.73	8
	Summer	6	4.19	0.75	4	7	4.38	0.76	4
	Autumn	14	4.58	0.74	10	16	4.35*	0.75	9
	Winter	12	4.05	0.75	10	12	4.06*	0.76	10
	Yr. av.	*49*	*4.19*	*0.75*	*35*	*49*	*4.28**	*0.75*	*31*
15	Spring	3	4.40	0.76	1	3	4.37*	0.72	2
	Summer	2	3.96	0.73	1	2	4.29*	0.74	2
	Autumn	3	5.01	0.74	3	6	4.78*	0.75	5
	Winter	7	4.52	0.76	4	5	3.95	0.76	4
	Yr. av.	*15*	*4.47*	*0.75*	*9*	*16*	*4.35**	*0.74*	*13*
				Young birds (2–4.5 months)					
29	Spring	1	4.77	0.72	1				
22	Spring	1	4.77	0.72	1				
				Old birds (60+ months)					
30	Spring	3	3.29	0.69	2				
20	Spring	2	2.96	0.75	1				
	Summer	1	3.87	....	..				
				Hybrids, 299 × Runt					
30	Spring	1	3.65	....	..	2	4.20	0.77	1
	Summer	7	3.60	0.73	3	2	4.27*	....	..
	Autumn	4	3.74	0.77	1	3	4.20	....	..
25	Spring	6	3.64	0.73	3	..	....	....	..
20	Spring	8	4.17	0.76	5	9	4.69*	0.76	4
	Summer	8	4.11	0.74	6	7	4.37*	0.72	3
	Autumn	13	4.46	0.74	8	10	4.70*	0.72	6
	Winter	16	4.03	0.74	10	13	4.66*	0.76	10
	Yr. av.	*45*	*4.19*	*0.75*	*29*	*39*	*4.61**	*0.74*	*23*
15	Spring	3	4.43	0.70	1	2	4.27	....	..
	Autumn	1	4.29	0.77	1	1	5.02	0.74	1
	Winter	8	4.22	0.76	4	8	4.82*	0.74	5
				Old birds (60+ months)					
30	Spring	..	....	....	..	1	2.65	0.73	1
	Summer	1	3.45	0.80	1				

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 58

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF PIGEONS OF RACE 267

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
RACE 267									
		Males				Females			
30	Spring	2	3.78	0.72	1	2	4.24*	0.76	1
	Summer	1	3.70	....	..	2	3.91*	....	..
	Autumn	..	....	....	..	1	3.81	....	..
20	Spring	7	3.93	0.73	4	8	4.45	0.78	3
	Summer	1	4.06	....	..	4	5.25*	0.73	1
	Autumn	5	4.67	0.74	3	2	5.24†	0.71	1
	Winter	2	3.62	....	..	7	4.36	0.77	2
	Yr. av.	*15*	*4.07*	....	..	*21*	*4.82*	*0.75*	*7*
15	Spring	3	4.85	0.73	1	5	4.91*	0.78	1
	Autumn	2	4.50	....	..	1	6.35	0.74	1
	Winter	1	4.69	....	..	2	4.59	0.72	1
HERMAPHRODITES—ADULTS									
30	Summer	1	3.62	....	..				
20	Spring	2	3.70	0.78	1				
	Summer	2	4.24	0.71	1				
	Winter	1	3.68	....	..				
15	Spring	1	4.43	0.73	1				
	Winter	1	3.76	....	..				
HERMAPHRODITES—OLD (60+ MONTHS)									
20	Spring	1	3.77	0.78	1				
15	Winter	1	4.21	....	..				

*Includes one or more measurements made on females within 50 hours of ovulation.

†The temperature used was 22°.

TABLE 59

Respiratory metabolism (calories per kilogram per hour) of young Carneau pigeons (7 to 10 weeks old) studied in the fasting and nonfasting condition (sexes combined)

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Nonfasting (2–11 hours after food)				Fasting (24 hours after food)			
30	Spring	65	4.56	0.79	25	20	4.46	0.75	8
	Summer	90	4.62	0.78	36	94	4.21	0.73	44
	Autumn	72	4.68	0.85	53	34	4.27	0.71	14
	Winter	47	4.64	0.75	23	25	4.47	0.73	10
	Yr. av.	*274*	*4.63*	*0.79*	*137*	*173*	*4.35*	*0.73*	*76*
25	Spring	20	4.85	0.92	10	30	4.15	0.72	16
	Summer	20	4.56	0.81	8	21	4.26	0.71	13
	Autumn	48	4.49	0.88	15	3	4.03	0.75	3
	Winter	..	....	....	..	2	3.81	....	..
	Yr. av.	*88*	*(4.64)*	*0.87*	*33*	*56*	*4.07*	*0.73*	*32*
20	Summer	8	5.14	0.95	4	8	4.75	0.71	4
	Autumn	11	4.88	0.96	5	9	4.54	0.75	6
	Winter	7	4.68	0.85	2	11	4.32	0.74	3
	Yr. av.	*26*	*(4.90)*	*0.92*	*11*	*28*	*(4.54)*	*0.73*	*13*
15	Summer	3	4.85	0.88	2	9	4.91	0.71	3
	Autumn	1	5.30	....	..	6	4.53	0.75	2

TABLE 60

Respiratory metabolism (calories per kilogram per hour) of Carneau pigeons and of hybrids of Carneau × Homer C

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
Carneau									
		Males				Females			
30. . . .	Summer. . . .	1	3.78	. . . .	. .	1	3.49	. . . .	. .
	Autumn. . . .	1	4.41	. . . .	. .	. .	. . . .	. . . .	. .
20. . . .	Spring.	7	3.60	0.71	3	6	4.03*	0.73	2
	Summer. . . .	3	4.27	0.72	1	4	4.22	0.70	3
	Autumn. . . .	1	4.18	0.76	1	1	3.36	0.75	1
	Winter.	10	4.14	0.72	5	4	3.94*	0.76	2
	Yr. av. . . .	*21*	*4.05*	*0.73*	*10*	*15*	*3.89**	*0.74*	*8*
		Old birds (60+ months)							
30. . . .	Spring.	1	3.16	0.74	1				
	Autumn. . . .	1	3.89	. . . .	. .				
20. . . .	Spring.	3	3.63	0.74	3				
	Summer. . . .	1	3.88	. . . .	. .				
Hybrids, Carneau × Homer C									
30. . . .	Spring.	1	3.01	0.82	1	1	3.45	0.77	1
	Summer. . . .	5	3.91	0.69	2	1	4.66	. . . .	. .
	Autumn. . . .	2	4.08	0.67	1	1	4.14	. . . .	. .
	Winter.	. .	. . . .	. . . .	. .	1	3.95	0.72	1
25. . . .	Spring.	1	3.48	0.77	1	1	3.64*	. . . .	. .
	Summer. . . .	2	3.86	. . . .	. .	. .	. . . .	. . . .	. .
20. . . .	Spring.	6	3.66	0.73	1	4	4.34*	0.73	2
	Summer. . . .	2	3.74	. . . .	. .	. .	. . . .	. . . .	. .
	Autumn. . . .	3	4.05	0.73	3	3	4.34	0.73	1
	Winter.	7	3.53	0.74	4	8	4.06*	0.74	4
15. . . .	Spring.	1	4.91	0.72	1	1	4.81	. . . .	. .
	Autumn. . . .	4	4.21	0.74	4	4	4.66	. . . .	. .

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 61

Respiratory metabolism (calories per kilogram per hour) of Homer C pigeons and of hybrids of Runt × Homer C

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
Homer C									
		Males				Females			
30	Summer	4	3.62	....	..	4	3.51	....	..
	Autumn	2	3.76	0.75	2	2	4.29	0.75	2
	Winter	1	3.62	....	..	..	....	....	..
20	Spring	14	3.71	0.73	10	12	3.80*	0.76	3
	Summer	4	4.12	0.73	2	3	4.56	0.71	2
	Autumn	9	4.43	0.75	6	8	4.39*	0.74	4
	Winter	9	3.66	0.75	6	8	3.80*	0.76	6
	Yr. av.	*36*	*3.98*	*0.74*	*24*	*31*	*4.14**	*0.74*	*15*
15	Spring	3	4.06	0.76	2	3	3.82	0.76	3
	Autumn	1	4.53	....	..	1	4.93	....	..
	Winter	2	4.52	0.72	1	1	3.79	0.78	1
		Old birds (60+ months)							
30	Spring	2	3.55	0.73	2	..	....	....	..
	Summer	2	3.59	0.74	2	..	....	....	..
	Autumn	2	3.62	0.79	2	..	....	....	..
	Winter	2	3.40	0.78	2	..	....	....	..
20	Spring	8	3.70	0.77	2	..	....	....	..
	Winter	1	4.13	....	..	1	3.84	....	..
Hybrids, Runt × Homer C									
30	Spring	8	3.99	0.72	2	..	....	....	..
	Summer	18	3.79	0.70	10	7	3.78*	0.70	5
	Autumn	7	3.91	0.76	4	2	4.08	....	..
	Winter	4	3.66	0.70	1	1	3.54	....	..
25	Spring	2	3.65	0.74	1	..	....	....	..
	Summer	1	4.05	...	..	..	....	....	..
	Autumn	2	4.50	....	.	..	....	....	..
20	Spring	14	4.03	0.73	6	14	4.09*	0.73	7
	Summer	9	3.80	0.73	5	9	4.62*	0.75	3
	Autumn	10	4.15	0.73	5	10	4.78	0.74	6
	Winter	15	3.95	0.75	7	14	4.32*	0.75	7
	Yr. av.	*48*	*3.98*	*0.74*	*23*	*47*	*4.45**	*0.74*	*23*
15	Spring	1	4.09	....	..	2	4.47	0.72	1
	Autumn	8	4.87	0.74	4	2	5.08	0.70	1
	Winter	3	4.59	0.75	2	3	4.80*	0.72	3

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 62

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF HOMER PIGEONS AND OF HYBRIDS OF HOMER × RACE 267

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
HOMER									
		Males				Females			
30	Spring	4	4.29	0.74	3	6	4.60*	0.75	4
	Summer	17	3.89	0.74	7	12	4.11*	0.76	6
	Autumn	10	4.13	0.74	4	7	4.12	0.76	4
	Winter	9	3.83	0.77	6	7	4.22*	0.77	5
	Yr. av.	*40*	*4.03*	*0.75*	*20*	*32*	*4.26**	*0.76*	*19*
20	Spring	39	4.05	0.74	23	45	4.64*	0.73	26
	Summer	15	4.19	0.73	10	17	4.78*	0.72	11
	Autumn	23	4.49	0.74	10	22	4.71*	0.72	11
	Winter	38	4.24	0.73	21	36	4.71*	0.73	18
	Yr. av.	*115*	*4.24*	*0.74*	*64*	*120*	*4.71**	*0.73*	*66*
15	Spring	8	4.48	0.75	5	10	5.01*	0.75	8
	Summer	2	5.05	0.74	2	1	4.82	....	..
	Autumn	4	5.03	0.76	2	8	5.36*	0.75	7
	Winter	8	4.47	0.74	3	11	4.98*	0.74	7
	Yr. av.	*22*	*4.76*	*0.75*	*12*	*30*	*5.04**	*(0.75)*	*22*
		Old birds (60+ months)							
30	Spring	6	3.47	0.74	2				
	Summer	4	3.34	0.67	2				
	Autumn	4	3.65	0.72	2				
20	Spring	12	3.79	0.72	6				
	Summer	4	3.91	0.77	2				
	Autumn	4	3.59	0.75	2				
HYBRIDS, HOMER × 267									
30	Summer	6	4.03	0.73	2	2	3.69	....	..
	Autumn	9	4.48	0.78	5	4	4.41*	0.72	2
	Winter	2	3.99	....	..	2	4.47*	....	..
25	Spring	2	4.43	0.75	1	..	....	....	..
	Summer	4	4.47	0.75	3	1	3.98	0.84	1
	Autumn	8	4.09	0.73	3	3	4.08	0.70	1
20	Spring	7	4.43	0.72	2	14	4.39*	0.75	5
	Summer	2	4.48	0.75	2	5	4.52*	0.72	4
	Autumn	9	4.39	0.75	5	6	4.74	0.75	3
	Winter	6	4.17	0.74	3	12	4.35*	0.73	8
	Yr. av.	*24*	*4.37*	*0.74*	*12*	*37*	*4.50**	*0.74*	*20*
15	Spring	2	3.93	....	..	4	4.46	0.79	1
	Autumn	2	5.13	0.74	2	1	4.57	0.74	1
	Winter	..	....	....	..	4	4.27*	0.76	3

*Includes one or more measurements made on females within 50 hours of ovulation.

TABLE 63

RESPIRATORY METABOLISM (CALORIES PER KILOGRAM PER HOUR) OF WHITE KING PIGEONS AND OF HYBRIDS OF HOMER × WHITE KING AND OF RUNT × HOMER

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
WHITE KING									
		Males				Females			
30	Spring	3	3.51	0.76	1	2	3.86*	0.77	2
	Summer	2	4.07	0.77	1	2	4.22	....	..
	Autumn	5	3.83	0.71	3	3	3.87	0.76	2
	Winter	2	3.68	....	..	2	3.92*	0.75	1
	Yr. av.	*12*	*3.77*	*0.75*	*5*	*9*	*3.97**	*0.76*	*5*
25	Spring	1	3.36	....	..	1	3.62	0.82	1
	Summer	1	4.03	0.70	1	..	....	....	..
	Autumn	2	3.98	0.73	2	..	....	....	..
20	Spring	6	4.01	0.74	5	6	4.31*	0.73	3
	Summer	..	....	....	..	1	4.17	....	..
	Autumn	6	3.87	0.73	4	5	4.26	0.70	1
	Winter	12	3.97	0.76	1	9	4.07*	0.76	6
	Yr. av.	*24*	*3.95*	*0.74*	*10*	*21*	*4.20*	*0.73*	*10*
15	Autumn	1	4.05	0.70	1	1	4.23	....	..
	Winter	2	3.86	....	..	2	3.82*	0.76	1
HYBRIDS, HOMER × WHITE KING									
30	Autumn	1	3.79	0.72	1	..	....	....	..
	Winter	2	3.89	....	..	2	3.76	....	..
25	Spring	2	3.87	0.72	1	2	3.82	0.76	1
20	Spring	2	3.84	0.74	1	2	4.43	0.74	1
	Winter	1	3.74	....	..	1	3.98*	0.75	1
		Old bird (75.0 months)							
20	Summer	1	3.90	0.74	1				

*Includes one or more measurements made on females within 50 hours of ovulation.

(*Continued on following page*)

TABLE 63—*Continued*

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
HYBRIDS, RUNT × HOMER									
		Males				Females			
30	Spring	1	3.71	0.74	1	3	4.28*	0.76	2
	Summer	14	3.79	0.71	7	11	3.84*	0.73	7
	Autumn	11	3.73	0.73	5	2	4.50	0.71	1
	Winter	..	....	....	..	1	4.27	0.75	1
25	Spring	2	4.10	0.75	1	2	3.82	0.75	1
	Summer	3	4.04	0.76	2	1	4.45	....	..
	Autumn	2	4.27†	0.72	2	..	....	....	..
20	Spring	10	4.02	0.72	6	10	4.31*	0.73	5
	Summer	6	4.06	0.71	3	8	4.47*	0.74	4
	Autumn	15	4.13	0.73	5	12	4.74*	0.73	7
	Winter	12	3.94	0.74	6	15	4.21*	0.74	7
	Yr. av.	*43*	*4.04*	*0.73*	*20*	*45*	*4.43**	*0.74*	*23*
15	Spring	2	4.30	0.75	1	2	4.49*	....	..
	Summer	1	4.51	....	..	1	4.66*	....	..
	Autumn	4	4.82	0.76	1	5	4.50*	0.76	1
		Young bird (4.5 months)							
30	Summer	1	3.84	0.82	1				

*Includes one or more measurements made on females within 50 hours of ovulation.

†The temperature used was 26°.

TABLE 64

Respiratory metabolism (calories per kilogram per hour) of miscellaneous pigeon hybrids (four types, all crossed with Magpie)

Temp. (°C.)	Season	No. of tests	Calories	R.Q.		No. of tests	Calories	R.Q.	
				Value	No.			Value	No.
		Males				Females			
30	Spring	4	4.24	....	..	3	4.05	0.77	1
	Summer	3	4.34	0.73	2	2	4.98	0.71	1
	Autumn	..	....	....	..	2	4.44	0.77	2
	Winter	..	....	....	..	3	4.31	0.78	3
25	Spring	..	....	....	..	1	4.55	....	..
	Summer	1	4.57	....	..	1	5.01	....	..
	Autumn	..	....	....	..	1	4.32	0.74	1
20	Spring	6	4.56	0.73	3	11	4.56*	0.71	5
	Summer	2	5.42	0.71	1	8	4.69	0.70	2
	Autumn	5	5.02	0.78	1	10	4.66*	0.76	5
	Winter	3	4.56	0.76	2	13	4.63*	0.74	4
	Yr. av.	*16*	*4.89*	....	*7*	*42*	*4.64*	*0.73*	*16*
15	Spring	2	4.96	0.80	1	1	5.00	0.78	1
	Autumn	1	4.85	0.80	1	4	4.84	0.71	2
		Young birds (3.0–4.2 months)							
30	Summer	1	6.01	0.73	1				
20	Spring	1	5.78	....	..				

*Includes one or more measurements made on females within 50 hours of ovulation.

14

SEASON AND TEMPERATURE AS FACTORS IN HEAT PRODUCTION IN DOVES AND PIGEONS

HISTORICAL

The possible existence of seasonal factors in human metabolism has received relatively slight attention, and such factors are disregarded entirely in current prediction standards for basal metabolism in man. The effects of climate, however, appear to be better understood; long residence in the tropics seems to decrease the basal metabolism. Temperature is apparently the predominating factor in this case, but other conditions such as light, humidity, air movement,[1] and temperature variability[2] are known to influence climatic adaptation. Du Bois[3] has summarized the results of investigations regarding temperature and other climatic factors in relation to season and basal metabolism. The earlier studies on seasonal variations, as such, were reviewed also in 1928 by Gustafson and Benedict.[4] These workers reported a higher basal metabolism during spring and early summer than during the winter months in measurements made on 20 college women. Of eleven seasonal studies which they reviewed, two gave no evidence for such changes; only in one case[5] was the metabolism reported to be higher in summer than in winter; this was for men living in Greenland, and the result was attributed mainly to the greater amount of sunlight during the long arctic days.

In most of the above-mentioned investigations only one or two subjects were used, and the results were often indefinite. Gessler,[6] however, reported his own basal metabolism for each month of the year, and this more elaborate study is noteworthy because of the close inverse correlation observed between metabolic rate and temperature. The rate was highest in January when temperature was lowest, and lowest in July when temperature was highest. A 3- to 4-hour period of adjustment to indoor temperature, followed by the customary rest period, was allowed before each test. This work has been criticized by Völker[7] on the ground that conditions were not well controlled; it has received favorable notice from others.[4,8] Deighton[8] writes as follows: "Gessler's curves correspond with such exactitude, however, that it is difficult to believe that there was not actually some effect under the conditions under which he worked—this was by short experiments while the subject was living a normal life. Any possible 'carry-over' effect of the cold weather outside in winter would certainly make itself felt under these conditions."

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[1] Sundstroem, E. S., Physiol. Reviews, 1927, vol. 7, p. 320.

[2] Ogle, C., and C. A. Mills, Amer. Jour. Physiol., 1932, vol. 103, p. 606.

[3] Du Bois, E. F., Basal metabolism in health and disease, pp. 190–197 (3d ed., Lea & Febiger, Philadelphia, 1936).

[4] Gustafson, F. L., and F. G. Benedict, Amer. Jour. Physiol., 1928, vol. 86, p. 43.

[5] Lindhard, J., Skand. Arch. f. Physiol., 1912, vol. 26, p. 221.

[6] Gessler, H., Pflügers Arch., 1925, vol. 207, p. 370.

[7] Völker, H., Pflügers Arch., 1926, vol. 215, p. 43.

[8] Deighton, T., Physiol. Reviews, 1933, vol. 13, p. 427.

Since a number of investigators have failed to find any seasonal difference in metabolism, it may be present only in certain subjects and not in others. This view receives indirect support from the work of Mason,[9,10] who found that about 62 per cent of the white women going to the tropics from a cooler climate showed a fall (of about 10 per cent) in basal metabolism; the other 38 per cent showed no change in metabolism but a rise in body temperature. Individual variations were also reported by Griffith and his associates[11] in regard to the season of maximal metabolism. This was generally found to occur in late winter, with the minimum in August; but in one subject the maximum was in April during two successive years.

In rats measured at the critical temperature, it now seems to be an established fact that the basal metabolism varies inversely with the previous environmental temperature, if the exposure is prolonged. The earlier investigations[12-16] pointed to such a relation, but it was sometimes not very obvious because of the short time of exposure to the conditioning temperatures or because of the small temperature difference. A few hundreds of tests on rats weighing 180 to 260 gm., and living at a temperature of 21° to 29°, indicated a somewhat lower basal metabolism during the summer months.[17]

Hemmingsen[15] stressed the importance of recording body temperature, since he observed only a slight depression in the temperature-corrected basal metabolism of rats which had lived 18 to 24 hours at 34.5° C., and no change in narcotized animals. Longer periods of exposure to warm air of low cooling power (high humidity and no movement) had been found earlier[18,19] to lower the basal metabolism of rats as much as 22 per cent. Prolonged adaptation to cold has likewise been effective. In rats kept at 7° to 12° C. during the greater part of each day, it was shown[20] that an exposure of 15 to 30 days was required to give the maximum increase in basal metabolism—in this case about 10 per cent, after

[9] Mason, E. D., Jour. Nutrition, 1934, vol. 8, p. 695.

[10] Mason, E. D., Amer. Jour. Trop. Med., 1940, vol. 20, p. 669.

[11] Griffith, F. R., Jr., G. W. Pucher, K. A. Brownell, J. D. Klein, and M. E. Carmer, Amer. Jour. Physiol., 1929, vol. 87, p. 602.

[12] Benedict, F. G., and G. MacLeod, Jour. Nutrition, 1929, vol. 1, p. 367.

[13] Ishida, K., Mitt. Med. Akad. Kioto, 1930, vol. 4, no. 3.

[14] Giaja, J., and S. Gelineo, Ann. de physiol., 1931, vol. 7, p. 163.

[15] Hemmingsen, A. M., Skand. Arch. f. Physiol., 1933–1934, vol. 68, p. 89.

[16] Gelineo, S., C. R. Soc. de biol., 1935, vol. 119, pp. 643–645, 645–647.

[17] Sherwood, T. C., Jour. Nutrition, 1936, vol. 12, p. 222.

[18] Sundstroem, E. S., Jour. Biol. Chem., 1925, vol. 63 (Proc. xli).

[19] Sundstroem, E. S., Univ. California Publ., Physiol., 1930, vol. 7, p. 103.

[20] Schwabe, E. L., F. E. Emery, and F. R. Griffith, Jr., Jour. Nutrition, 1938, vol. 15, p. 199.

correcting for body-temperature changes. Ring[21] demonstrated an even greater increase (16 per cent, temperature-corrected) with rats which had lived at 0° to 5° for 3 weeks or longer. The later investigations of Gelineo[22] on heat production at 36° C., by rats which had been living at low and medium temperatures, demonstrated essentially the same result; also that, in the zone of thermolysis, body temperature can be maintained constant although the intensity of heat production is different.

In rabbits subjected to a low temperature for 2 to 3 weeks, Lee[23] found that the basal metabolism at 28° was higher by as much as 26 per cent than in animals from a warm environment. Moreover, in the study of Ogle and Mills,[2] rabbits adapted to living in a cool environment were reported to have greater ability than warm-adapted animals to maintain a normal body temperature and to utilize their muscle glycogen quickly in response to cold.

Kayser[24] measured the metabolic rate in a species of dormouse, the lerot, after adaptation to life at 20° and 8° C. The basal metabolism, determined at about 28°, was found to be 696 calories per 24 hours in the first case, 908 calories in the second; the maximal metabolism (measured at 1° C.) was also higher in the second case than in the first.

Birds have been shown to respond in a similar manner to changes in temperature of the environment. Kayser[25] found that the basal metabolism of 3 pigeons kept for 31 days in an incubator at 28° was 3.695 calories per kilogram per hour, compared with 5.232 calories for 8 control birds at room temperature; but the effect of confinement in depressing metabolism was apparently not taken into account, and some of the measurements were not made at night. Gelineo[26] measured the metabolism of a greenfinch (*verdier*) at five different temperatures, first after living for a month at 14–20°, and again after 6 weeks in a large, well ventilated thermostat at 29–32°. There was a shift of the zone of thermal neutrality from 30–31° in the cold-adapted to 33–35° in the warm-adapted bird, with a drop in basal metabolism of 32 per cent. In the warm-adapted bird the metabolic rate was lower at each temperature of measurement between 28° and 37°, especially in the upper range; also, polypnoea first appeared at a temperature 3° higher than in the cold-adapted bird.

Very little is known in regard to the effect of seasonal factors other than temperature upon metabolism in animals. The basal metabolism of domestic animals, from which most of our animal data have been obtained, sometimes shows considerable fluctuation from one season to another, or from day to day (ruminants). These animals are more exposed to extremes of heat and cold than man, and do not possess man's ability to put on and remove body covering. Greater changes in body temperature with season may perhaps occur in domestic animals than in man, since they are known to show diurnal variations from 2 to 5 times as great as in man.[8] These and other factors, such as change of diet, the reproductive functions, and light, as well as temperature, may influence the metabolism of animals more at certain seasons than at others.

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[21] Ring, G. C., Amer. Jour. Physiol., 1939, vol. 125, p. 244.

[22] Gelineo, S., Bull. Acad. sci. math. nat., Belgrade, 1940, B, no. 6, p. 149.

[23] Lee, R. C., Jour. Nutrition, 1941, vol. 23, p. 83.

[24] Kayser, Ch., Ann. de physiol., 1939, vol. 15, p. 1087.

[25] Kayser, Ch., C. R. Soc. de biol., 1929, vol. 101, p. 708.

[26] Gelineo, S., C. R. Soc. de biol., 1934, vol. 117, p. 40.

From a study of 5 male guinea pigs throughout a year, Maignon[27] concluded that there are two periods of highest metabolism, in spring and autumn, corresponding to the periods of greatest activity of the sex glands. The metabolic rhythm was partly suppressed in 5 castrated males. He observed[28] a similar cycle of metabolism in 1 fasting and 1 nonfasting dog, with a less apparent increase in rate in autumn than in spring; the cycle was likewise observed[29] in 1 control animal and in 3 castrates followed through all or parts of one year.

It is known that there is a distinct rise in the basal metabolism of sheep[30,31] and of cattle[32] when they are transferred to pasture. Ritzman and Benedict[32] thought that a seasonal factor (other than diet) might be involved because, of 6 cows maintained on a uniform diet of hay and grain, 5 showed a distinctly higher basal metabolism in May than during late winter. Sheep have been shown to have a maximum metabolism associated with shearing, gestation, lactation, and change to pasture in the spring, with a minimum in autumn.[33] This metabolic cycle was also present in castrated males (wethers) and in females which were not bred. A similar cycle was observed in goats.[34] In controlled experiments on young nonlactating goats it was found[35] that the period of highest resting metabolism and greatest gain in weight was in early spring; the lowest metabolism was in the autumn. In mature goats it is known that the greatest number of births occurs in early spring, when the level of metabolism is high in young goats, and the greatest number of conceptions occurs in autumn. It should be noted that in these studies on sheep and goats, there appear frequently in the graphs smaller increases in metabolism during mid-autumn, which are suggestive of the condition found by Maignon and others in smaller mammals.

The seasonal temperature effect on the basal metabolism of rats has been mentioned. In addition, it has been found by Cori and Cori[36] that the respiratory quotient of rats under basal conditions is usually above 0.70 between September and May and below 0.70 during the summer. The low R.Q. of summer was associated with ketonuria (a change in fat metabolism) and not with temperature, since exposure to heat during the winter did not lower the R.Q. values appreciably.

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[27] Maignon, F., C. R. Acad. sci., 1913, vol. 156, p. 347.

[28] Maignon, F., and A. Painvin, C. R. Acad. sci., 1929, vol. 188, p. 573.

[29] Maignon, F., and J. Guillon, C. R. Acad. sci., 1931, vol. 192, p. 1410.

[30] Benedict, F. G., and E. G. Ritzman, Arch. f. Tiernährung u. Tierzucht, 1931, vol. 5, p. 1.

[31] Lines, E. W., and A. W. Pierce, Com. of Australia Council for Sci. and Indust. Res. Bull. 55, 1931.

[32] Ritzman, E. G., and F. G. Benedict, The nutritional physiology of the adult ruminant, p. 136 (Carnegie Inst. Wash. Pub. 494, 1938).

[33] Brody, S., W. C. Hall, A. C. Ragsdale, and E. A. Trowbridge, Missouri Agric. Exper. Sta. Res. Bull. 176, 1932.

[34] Brody, S., Missouri Agric. Exper. Sta. Res. Bull. 283, 1938.

[35] Brody, S., Missouri Agric. Exper. Sta. Res. Bull. 291, 1938.

[36] Cori, C. F., and G. T. Cori, Jour. Biol. Chem., 1927, vol. 72, p. 615.

Winchester[37] determined the fasting metabolism in 27 New Hampshire pullets, and found it to be distinctly higher in winter and spring than in summer and autumn. The rate varied inversely with the temperature of the environment, which ranged from 2° C. in winter to 33° C. in summer.

Dontcheff and Kayser[38] made monthly measurements of the basal metabolism of 3 pigeons exposed to natural variations in outside temperature (from $-0.8°$ to $20.5°$), and found that the rate was high during winter, low in early spring, and lowest in autumn; it was moderately high in late spring and summer, with a brief maximum recorded in July for which no explanation appeared.

According to the results obtained by Riddle and his associates[39] on Tippler pigeons, the basal metabolism was highest in the autumn and lowest in the spring. The birds were confined in houses partly heated from November until May, and had access to unfiltered sunshine during the remainder of the year. The higher metabolic rate in summer as compared with spring was attributed to the larger amount of light rays (particularly ultraviolet) available to the birds at this season; the still higher rate in autumn (above that in summer) was attributed to increased thyroid activity resulting from the low temperatures which prevailed before the resumption of artificial heating in late autumn and winter. Only measurements made at 15° showed a different or opposite relation between summer and autumn metabolism values, and this exceptional result was thought to reflect differential stimulating effects of this very low temperature. During autumn the birds had been living in air of great cooling power, their mechanisms of heat production and heat loss had been adjusted to this high degree of cooling power, and when they were placed in the metabolism chamber at 15°, this temperature, therefore, had relatively *little* stimulating effect; during summer the birds had been living at a high external temperature, their mechanisms of heat production and heat loss were then adjusted to this low degree of cooling power, and when they were placed in the metabolism chamber at 15°, this temperature had a relatively *great* stimulating effect.

It will be found that the conclusions just stated are confirmed, and extended to other races, by the data contained in this volume. The probable causes of the observed seasonal differences, and also of seemingly aberrant effects of low temperatures, are indicated in the preceding paragraph. Gonad activity in these birds is at a maximum in spring and at a minimum in autumn; thyroid activity shows essentially the reverse relation, particularly in doves.[40] Many facts indicate that the metabolic levels are associated with thyroid rather than with gonad function.

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[37] Winchester, C. F., Missouri Agric. Exper. Sta. Res. Bull. 315, 1940, pp. 1–52.

[38] Dontcheff, L., and Ch. Kayser, Ann. de physiol., 1934, vol. 10, p. 285.

[39] Riddle, O., G. C. Smith, and F. G. Benedict, Amer. Jour. Physiol., 1934, vol. 107, p. 333.

[40] Riddle, O., Amer. Jour. Physiol., 1925, vol. 73, p. 5.

Experimental Results

Though the tabulated data of the previous chapter provide this information in another form, it will be obvious that the nature and extent of effects of season, and of temperature of measurement, can best be shown in the form of curves or graphs. Again, in some cases, relative rates of heat production in the two sexes and in hybrids are best observed in similarly constructed curves. It is to be noted, however, that only a few representative parts of the data are thus shown; the present survey is based on the tabular material presented in the preceding chapter.

All data obtained during the months of December, January, and February were classified as "winter" values; those of June, July, and August as "summer" values; those of the intervening months as "spring" and "autumn." It is thus obvious that some measurements made on consecutive nights were classified under different seasons; this contributes to the variability of the tabulated averages, but more especially to that of averages of small numbers of measurements. Moreover, this method of classifying the data unavoidably tends to minimize or obscure the full extent of change of metabolic rate during the annual cycle. On the other hand, presentation of the data on a monthly basis was impracticable.

Data from Dove Races and Hybrids

Figures 175 to 179 show that, as a rule, the rate of heat production is highest in the autumn, slightly lower in summer, and still lower in winter and spring. The rule applies alike to races and to hybrids. This series of graphs, like that similarly prepared for pigeons (figs. 180–183), indicates that the rule which describes the relation of season to metabolic rate is more often broken in measurements made at 15° C.; moreover, in such measurements the values obtained for *summer* are usually the most irregular or aberrant. These irregularities are in part a consequence of the fact that a smaller number of measurements were made at 15° C. (and also during the summer) than at higher temperatures. It seems probable, however, that a part of these irregularities are ascribable to an insulting action of this low temperature upon birds currently living at considerably higher (highest in summer) environmental temperatures.

The continuous increase in the metabolic rate with decrease in temperature is well shown in these graphs. In the preceding chapter it was observed, however, that lower temperatures affect the heat production of some racial and hybrid types much more than that of other types. On this point some specific figures may be cited. From the tabulated data it can be calculated that the metabolism at 15° exceeded that at 20° C. by percentages as small as 9.0 (in *N2* × *62*), 13.2, and 13.7 (races *W* and *B*); and also by percentages as large as 19.9 (race *72*), 19.7 (*B* × *72*), and 19.6 (race *62*). Among pigeon types these values showed even greater differences; percentages as small as 4.1 (Runts) and 7.5 (*S.1-R*, ataxic) and as large as 18.5 (*M* × *T*), 18.3 (Magpies), and 15.7 (scragglies) were obtained. The fact that change of temperature produces unequal effects on the heat production of the two sexes will be considered in chapter 15.

In figures 175 and 176 the data for males and females are plotted separately. In

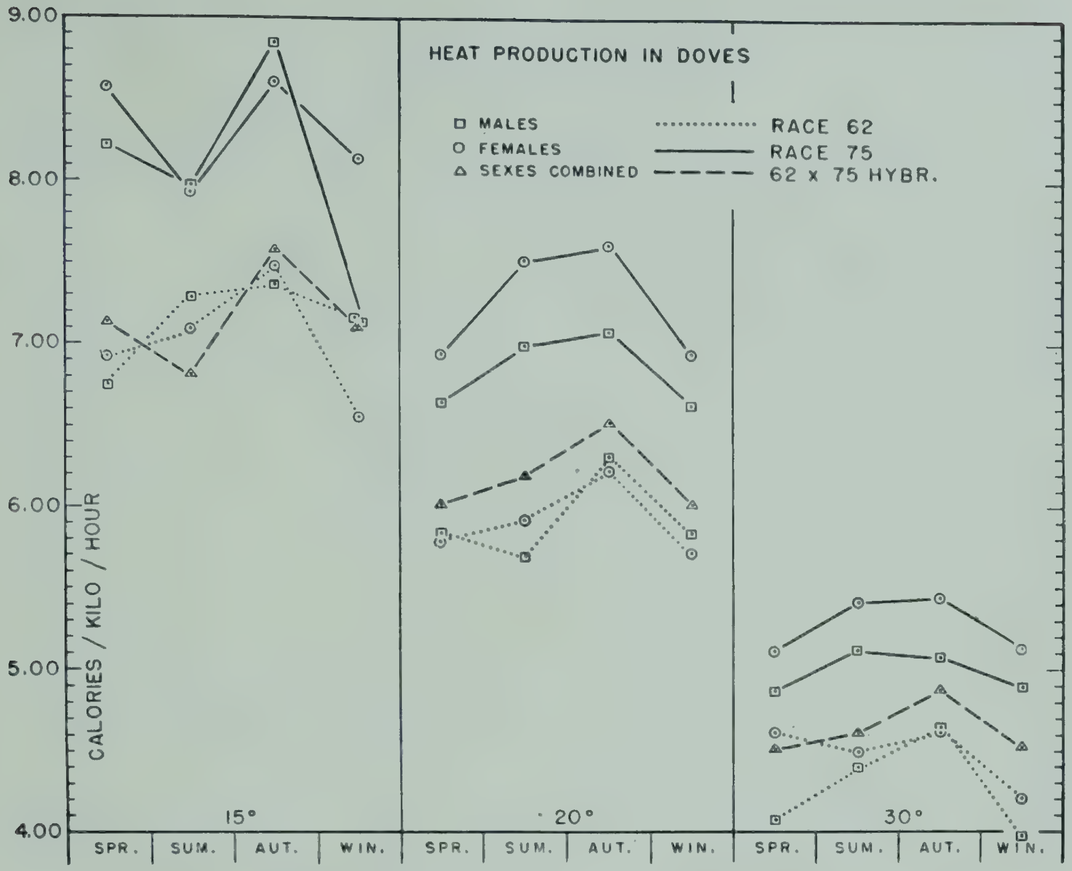

FIG. 175. Effects of season and temperature on the metabolism of races *62* and *75* and their hybrids.

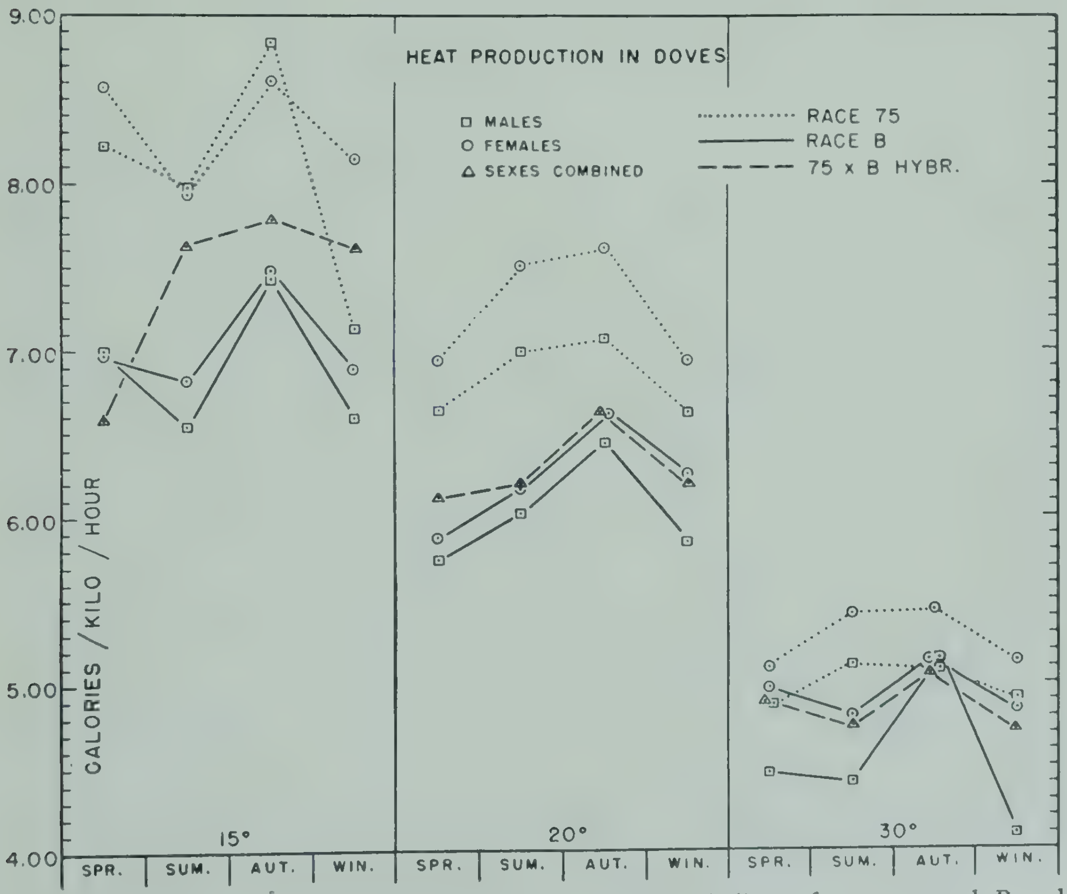

FIG. 176. Effects of season and temperature on the metabolism of races *75* and *B* and their hybrids.

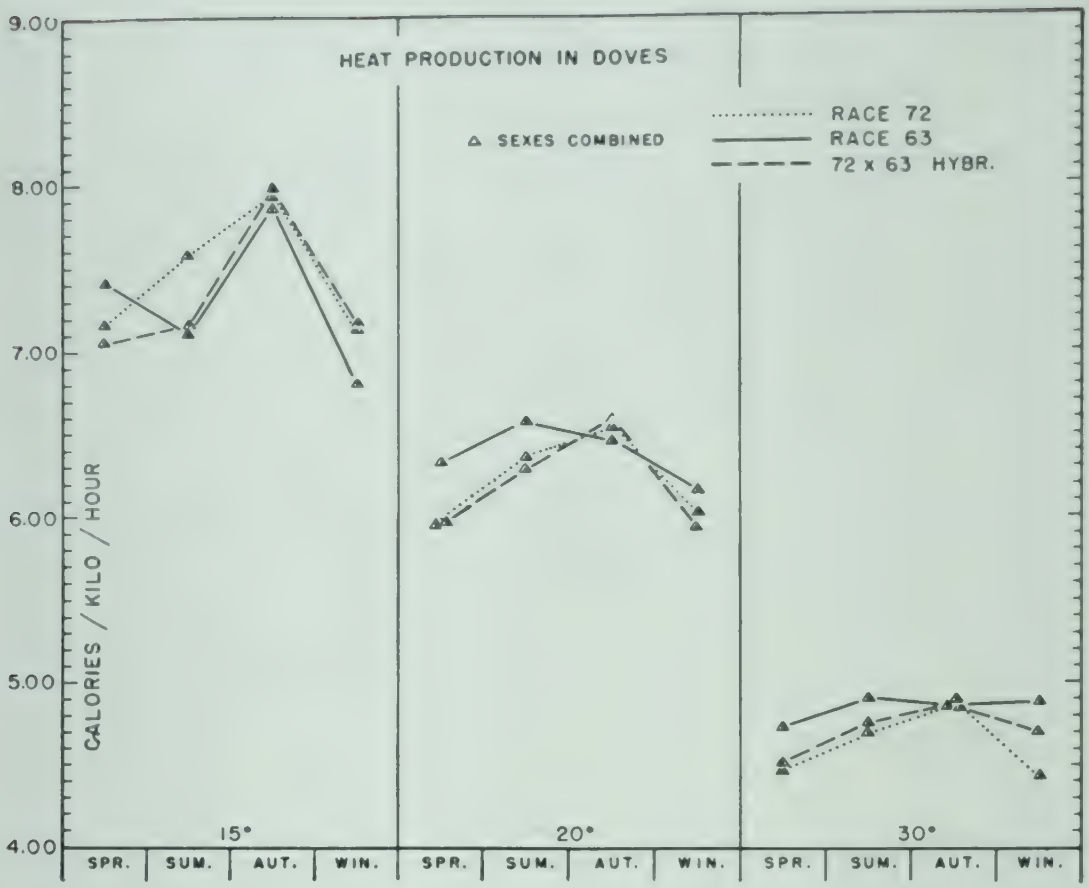

FIG. 177. Effects of season and temperature on the metabolism of races *72* and *63* and their hybrids.

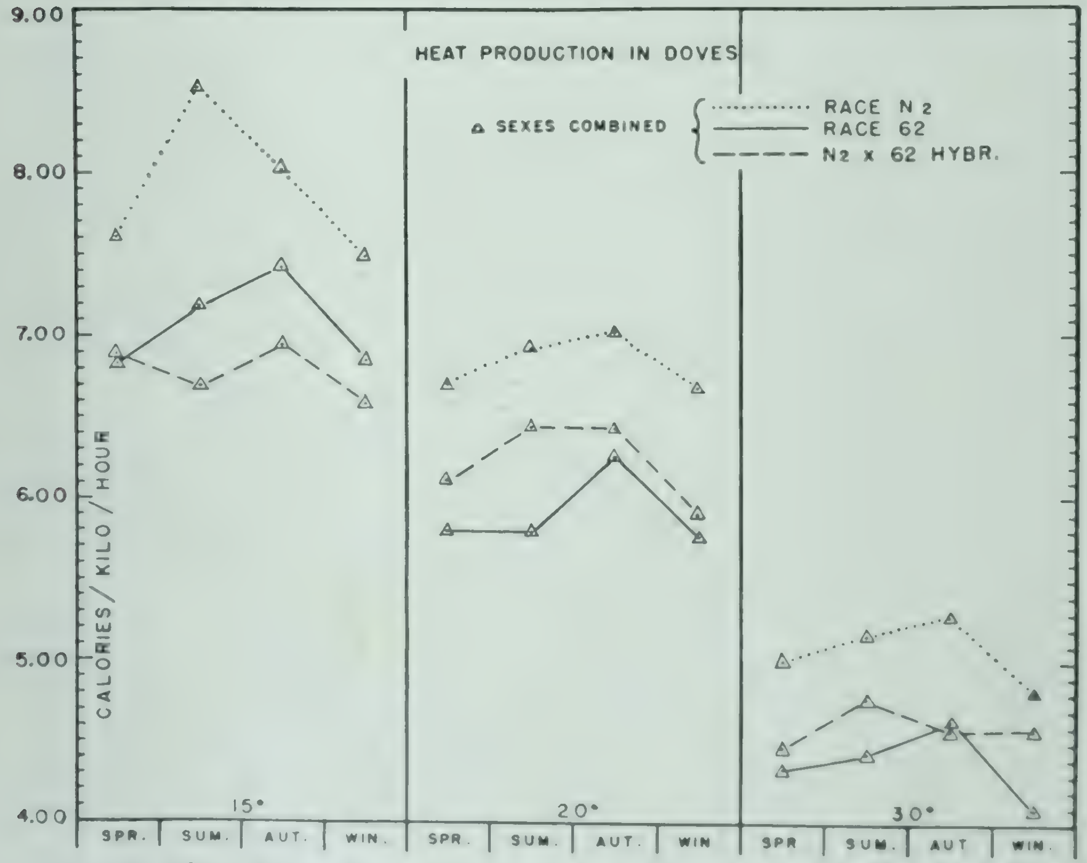

FIG. 178. Effects of season and temperature on the metabolism of races *N2* and *62* and their hybrids.

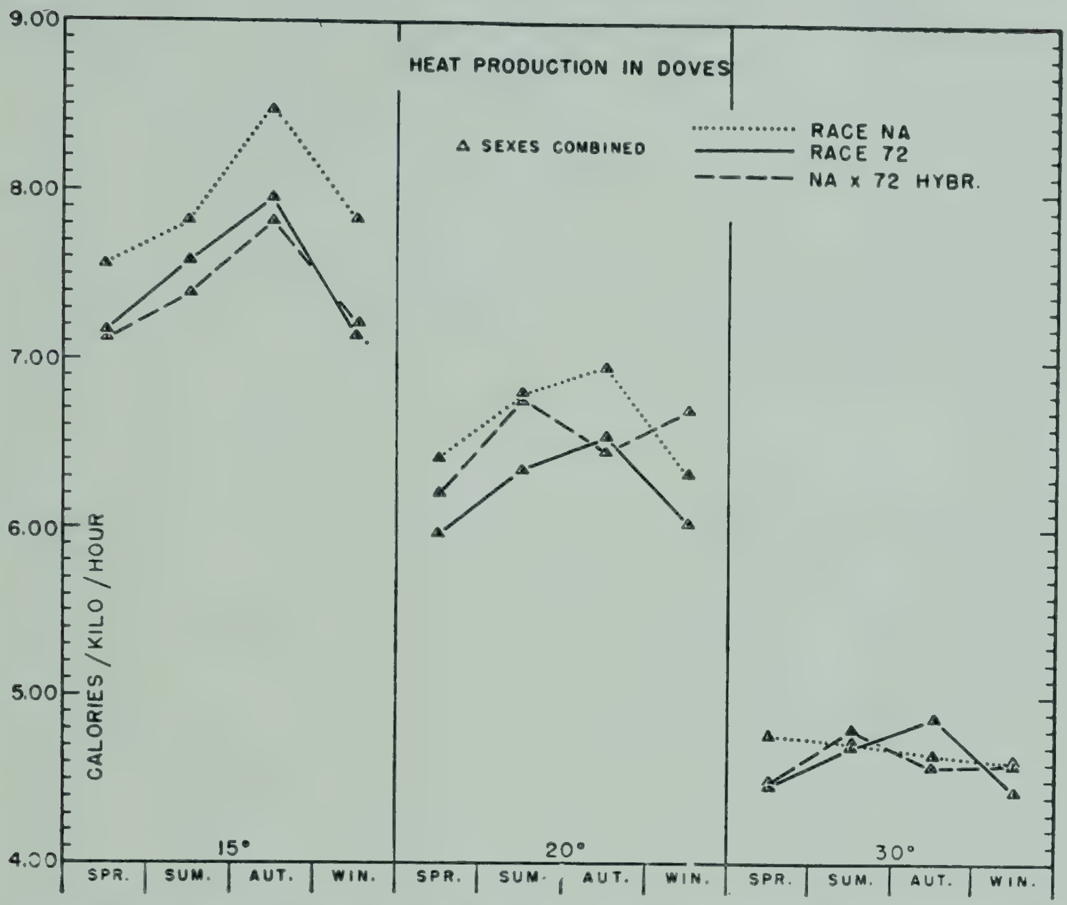

FIG. 179. Effects of season and temperature on the metabolism of races *NA* and *72* and their hybrids.

figures 175 to 179 the data for hybrids are plotted alongside the curves which describe the heat production of the two parental races. In these several graphs the rate of heat production in the hybrids is intermediate to the rates found for the parental races. That condition was usual, but apparently it was not invariable. On this point the data of figures 175 and 178 are of rather special interest. The curves show details of values obtained for the two dove races (*75* and *62*) which, respectively, had the highest and the lowest basal rates, and for the hybrids derived from them (fig. 175) and from *N2* and *62* (fig. 178). These hybrids show an intermediate value at the three temperatures; in each case, however, their rate is somewhat nearer to that of race *62;* and it is only at 15°, and in the summer season, that an average value for the hybrids falls below an average obtained from race *62*. Another interesting result is shown in figure 179.

For 13 types of doves (7 races, 6 hybrids) for which adequate data were available (tables 14–44), the relative role of season in metabolism, at the three temperatures used and for both sexes, was calculated. The "yearly average" metabolism obtained for one sex at a particular temperature was assigned a value of 400 per cent, since it represents four seasons; thereafter, the proportion of 400 per cent which was contributed by measurements made in each of the four seasons (three temperatures and two sexes) was ascertained. Thus, in one race the following percentages were obtained: spring, 99; summer, 101; autumn, 104; winter, 96. When the values thus obtained for the 13 types are averaged, the relative role of the seasons in the heat production of doves is found to be as follows: spring, 97 (extremes, 95–99); summer, 101 (98–104); autumn, 104 (101–108); winter, 98 (96–101).

The data just summarized fully confirm the above-cited conclusions of Riddle, Smith, and Benedict[41] concerning heat production in Tippler pigeons; and the reasons assigned for these seasonal variations in the Tippler pigeons seem entirely applicable to doves.

Data from Pigeon Races and Hybrids

Figures 180 to 183 graphically present for pigeons data of the same nature as those described immediately above for doves. It will be noted that the relation of season to rate of heat production is much less evident in pigeons than in doves. From the data of tables 45 to 63, however, it can be learned that 11 pigeon types were measured fairly adequately during spring and autumn at all the three temperatures. The autumn values exceeded those of spring in 10 of the 11 types at 30°, in 10 at 20°, and in 8 at 15° C. The average amounts by which the 11 autumn values exceeded those of spring were as follows: at 30°, 4.7 per cent; at 20°, 7.8 per cent; at 15°, 4.6 per cent.

In considering other aspects of the data shown on these graphs it may be recalled that, although the heat-production values were calculated on a basis of body weight, it is only in one graph (fig. 181) that body weight of the two parental types differs considerably. Figure 183 adequately shows that scraggly pigeons respond to lower temperatures by an extraordinary increase in their rate of heat production. The curves also indicate that heat production in ataxic and normal (*SA-R*) pigeons is essentially equivalent at all temperatures.

From a part of the present data for Tippler pigeons (table 44) Riddle, Smith, and Benedict[42] concluded that the percentage metabolism change per degree of temperature change is a function of *season*, and of the particular range of the thermometric scale which is used for measurement. That conclusion is supported by many data contained in tables 14 to 63. Only a single specific reference will be made to those data. The summer values obtained on Tipplers (table 45) at three different temperatures provide the following information. Decreasing the temperature from 30° to 20° C. increased the rate of heat production by only 3.8 per cent. But the rate of heat production which prevailed at 20° C. was increased by 19.8 per cent by reducing the temperature to 15° C.

SUMMARY AND CONCLUSIONS

Season is associated with marked changes in the rate of heat production of ring doves. Summer values are intermediate to those of winter and autumn.

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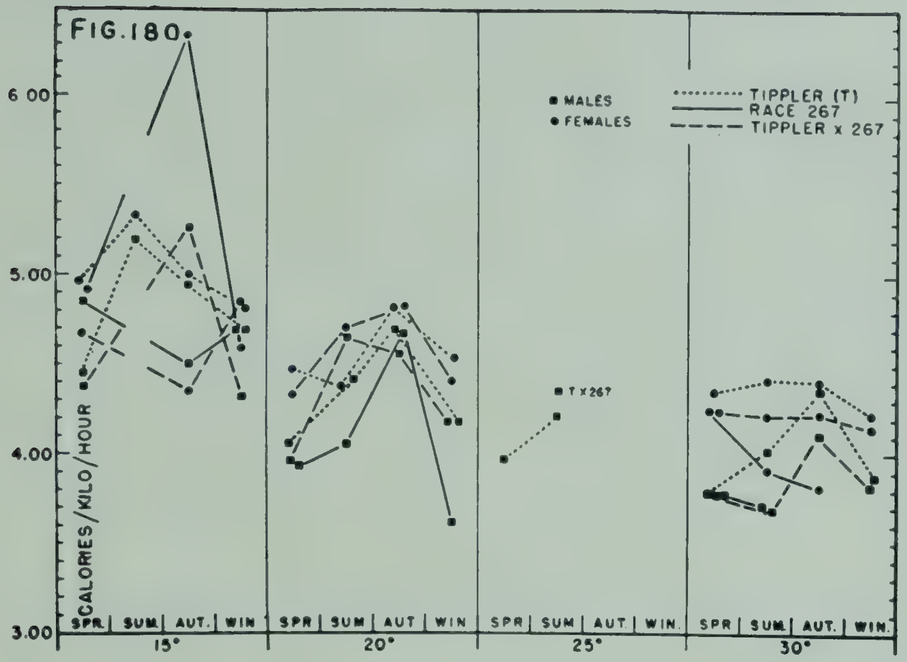
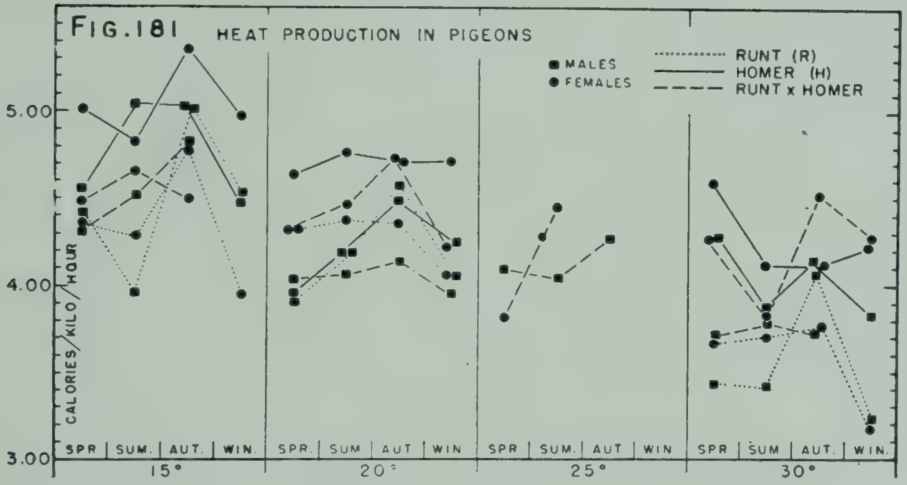
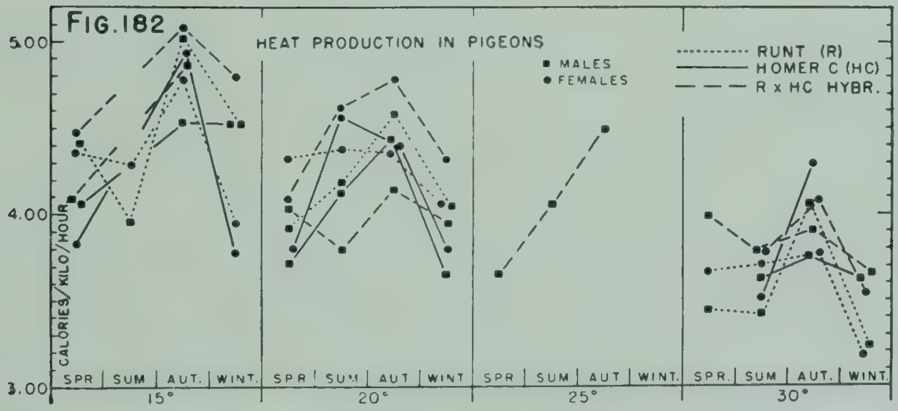
[41] See footnote 39 and the associated statement in the text.

[42] See footnote 39.







Figs. 180–182. Effects of season and temperature on the metabolism of 5 pigeon races and 3 types of hybrids. Separate curves show values obtained for the two sexes. The hybrids shown in figure 180 are otherwise regarded as a "hermaphrodite-producing race." At all temperatures highest rates of heat production tend to occur in autumn.

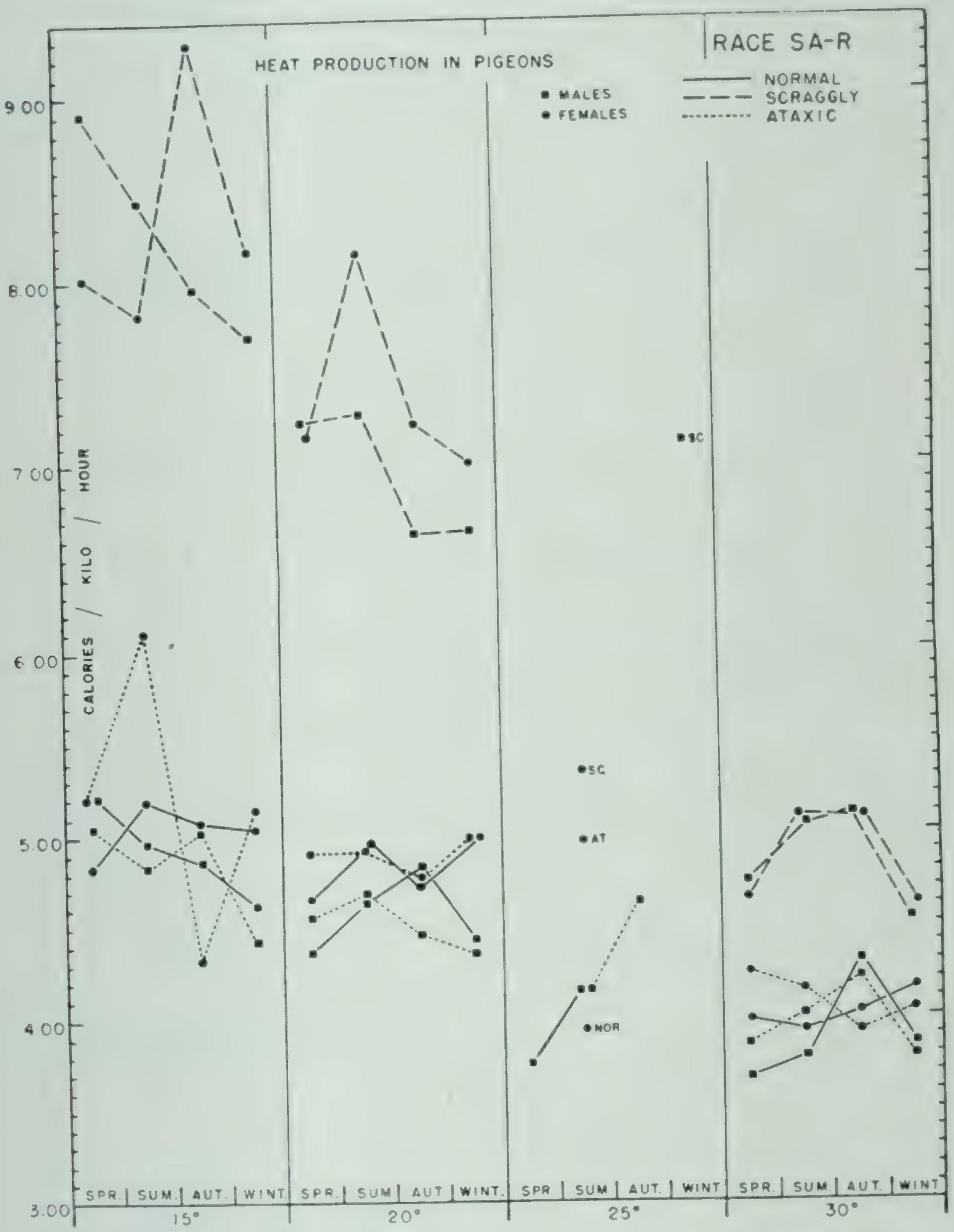


Fig. 183. Effects of season and temperature on 3 types of pigeons of race *SA-R*

Autumn values exceed those of spring by 7 per cent and those of winter by 6 per cent. These values do not represent the extremes of the annual cycle, but merely the difference in averages obtained from 3-month periods. The actual extreme difference associated with the annual cycle was probably more than 8 and less than 12 per cent.

Season had a less consistent effect on rate of heat production in pigeons than in doves. The average autumn heat production of 11 pigeon types exceeded that of spring by 4.7 per cent at 30° C., 7.8 per cent at 20° C., and 4.6 per cent at 15° C.

The seasonal differences observed in these tests are believed to reflect, to a considerable extent, the conditions of housing and confinement. The birds were maintained in partly heated houses from November until May, and had free access to sunshine (ultraviolet) during the remainder of the year. The higher metabolic rate for summer as compared with spring is attributed to the larger amount of light rays (particularly ultraviolet) which were available to these birds at this season; the still higher rate for autumn (above that for summer) is attributed—as in an earlier study by Riddle, Smith, and Benedict—to increased thyroid activity resulting from the low temperatures which prevailed prior to the resumption of artificial heating in late autumn and winter.

In measurements made on many pigeon breeds it is found that the extent to which heat production is increased by lower temperatures depends, first of all, on race. Secondly, it depends on the season at which the measurement is made. Thirdly, it depends on the part of the thermometric scale employed. For example, during summer, the heat production of Tippler pigeons was increased by only 3.8 per cent by reducing the temperature from 30° to 20° C.; but the value obtained at 20° was increased by 19.8 per cent by reducing the temperature to 15° C. The sex factor, in its relation to metabolic rate under temperature changes, is discussed in the following chapter.

15

THE ROLE OF SEX IN HEAT PRODUCTION

Historical

It may be noted that in general, in mammals including man, the basal metabolism of the male is higher than that of the female. The figures for the domesticated albino rat, which has been studied rather extensively for sex differences, are given[1] as 600 calories per square meter per day for the male, and 571 for the female; another investigation[2] obtained 800 for the male, 720 for the female. Other studies[3] obtained, for adults, about 17 per cent lower values in females than in males; for young rats, 5 per cent lower in females; and for rats in the second and third years, higher values in males than in females. For the wild Norway rat[4] the data are also suggestive of a higher level of metabolism in the male. In older albino rats (800 days and above) the values obtained[5] were 710 for males and 703 for females. It may be that the sex difference in metabolism in the rat becomes less in old age, as it does in man. This inference is not substantiated, however, by the work of Davis,[6] who followed the metabolism of 136 rats between the ages of 1 and 30 months. He showed that estrus raised the metabolic rate of females above that of the males; but that in nonestrous females the rate was distinctly lower than in males, and remained so from about the third month onward.

The basal metabolism of the rabbit was found[7] to be slightly higher in the male than in the female. For sheep[8] measured under standard conditions (fasting, but standing), the figures reported for heat production indicate a somewhat lower rate in males than in females. On the basis of later experiments, however, it was concluded[9] that after the sixth month male sheep have a slightly but probably not significantly higher metabolism than female sheep. Pierce[10] found only an insignificant sex difference in the metabolism of sheep. The basal metabolism of the goat was given[11] as 880 calories per square meter for a single buck, and

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[1] Mitchell, H. H., and G. G. Carman, Amer. Jour. Physiol., 1926, vol. 76, p. 385.

[2] Benedict, F. G., and G. MacLeod, Jour. Nutrition, 1929, vol. 1, p. 367.

[3] Horst, K., L. B. Mendel, and F. G. Benedict, Jour. Nutrition, 1934, vol. 7, p. 277; 1935, vol. 8, p. 139.

[4] Benedict, F. G., and J. M. Petrik, Amer. Jour. Physiol., 1930, vol. 94, p. 662.

[5] Benedict, F. G., and H. C. Sherman, Jour. Nutrition, 1937, vol. 14, p. 179.

[6] Davis, J. E., Amer. Jour. Physiol., 1937, vol. 119, p. 28.

[7] Lee, R. C., Jour. Nutrition, 1939, vol. 18, p. 473.

[8] Ritzman, E. G., and F. G. Benedict, Univ. New Hampshire Agric. Exper. Sta. Tech. Bull. 43, 1930.

[9] Ritzman, E. G., and F. G. Benedict, Univ. New Hampshire Agric. Exper. Sta. Tech. Bull. 45, 1931.

[10] Pierce, A. W., Com. of Australia Council for Sci. and Indust. Res. Bull. 84, 1934.

[11] Ritzman, E. G., L. E. Washburn, and F. G. Benedict, Univ. New Hampshire Agric. Exper. Sta. Tech. Bull. 66, 1936.

680 for 6 does. The last-cited study recorded data which indicate a considerably higher metabolism in 1 boar than in 3 sows; also, a slightly higher level for steers than for cows. In a later report from the same laboratory[12] it was stated that the metabolism of 5 fasting adult bulls was much in excess of that of cows, except when the latter were lactating. The basal metabolism of a Percheron stallion was found to be greater than that of a Percheron mare.

Others[13] had reported earlier that the *resting* metabolism (after 8 to 12 hours of fasting) of growing cattle was 10 per cent higher in males than in females; and that of swine, 20 per cent greater in males, probably because of the relatively large amount of fat in the female of this species. Similar differences in *basal* metabolism between the sexes were also found. In growing cattle the metabolism of the female was reported[14] to be greater than that of the male until a weight of 150 kg. was attained, when the rates became equal; thereafter the metabolism of the male rose continuously while that of the female declined with increasing age.

The existence of a sex difference in human metabolism has long been recognized. Studies on large numbers of normal subjects by Harris and Benedict[15] and by Boothby, Berkson, and Dunn[16] have indicated that the basal or standard metabolism is higher (3 to 10 per cent) in males than in females at all ages between 6 and 75 years.

Only recently, however, was it observed that in a few adequately tested instances the magnitude of this difference depended on the environmental temperature. In the Sage calorimeter, a comparison was made[17,18] of heat production and elimination in 8 women and 2 men in the nude condition, at temperatures between 22° and 36°. The rectal temperature of the subjects remained nearly constant throughout the temperature range; the skin temperatures varied directly with outside temperature, somewhat more in the women than in the men. In the colder zone (22–27° C.) the heat production was approximately the same in the women and the men. Above 27° the rate remained constant in the men, but showed a marked drop in the women until it attained at 31° an average value about 12 per cent lower than in the men. This fall in metabolism in the women was accompanied by a corresponding reduction in heat loss, and represents a "chemical regulation" of metabolism. The sex factors concerned in these results are important, and they are discussed by the authors[17] as follows:

> In (nearly) all adjustments to changes in the thermal environment the women have a physiological advantage. The comfort zone, in which the heat loss and heat

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[12] Ritzman, E. G., and F. G. Benedict, The nutritional physiology of the adult ruminant (Carnegie Inst. Wash. Pub. 494, 1938).

[13] Brody, S., W. C. Hall, A. C. Ragsdale, and E. A. Trowbridge, Missouri Agric. Exper. Sta. Res. Bull. 166, XVII, pp. 5–44; XVIII, pp. 45–65.

[14] Brody, S., Missouri Agric. Exper. Sta. Res. Bull. 143, 1930, p. 48.

[15] Harris, J. A., and F. G. Benedict, A biometric study of basal metabolism in man (Carnegie Inst. Wash. Pub. 279, 1919).

[16] Boothby, W. M., J. Berkson, and H. L. Dunn, Amer. Jour. Physiol., 1936, vol. 116, p. 468.

[17] Hardy, J. D., and E. F. Du Bois, Proc. Nat. Acad. Sci., 1940, vol. 26, p. 389.

[18] Hardy, J. D., A. T. Milhorat, and E. F. Du Bois, Jour. Nutrition, 1941, vol. 21, p. 383.

production are equal, extends over a range of about 6° for women instead of 2–3° for men. The most important factor is the fall in heat production of women in warmer environments. Another factor is the thicker layer of insulation against cold. A third factor is a slightly better adaptation of skin temperature to meet thermal changes in the environment. In cool air women, lightly clad, may be comfortable when the men need woolen clothing. In the warm zone long before the women have started to perspire or even "glow" the men may be covered with beads of sweat.

Sex differences have been reported for the basal metabolism of birds, but the various reports, even for the same species, are somewhat contradictory. In fowls,[19] the Rhode Island Red male was found to have a higher basal metabolism than the female; results were similar[20] for Plymouth Rock chickens. A basal metabolism (measurements made at night) 34 per cent higher in the cock than in the hen was reported by Herzog,[21] who obtained in geese a 12 per cent lower metabolism in the male than in the female. Others reported either an insignificantly lower basal metabolic rate for Rhode Island Red cocks than for hens,[22] or a value about 9 per cent higher for mature males than for females.[23]

Determinations made by Riddle, Christman, and Benedict[24] on ring doves previously kept for 24 hours at each environmental temperature showed a higher rate for males than for females at 20° and at 15°, but a lower rate at 30° C. These investigators expressed the opinion that the measurements at 30°, although giving minimal figures, were obtained under nonphysiological conditions which affected the male more than the female. The values cited were calculated on a weight basis, and the authors suggested further that calculations based on surface area, and corrections made for the temporary increase of heat production at ovulation, should both tend to reduce the observed heat production in females. These several conclusions will be found to have important bearing on the interpretation of the results obtained in the present study. In a later investigation[25] on mourning doves a higher metabolism was found in the male than in the female at all the above-mentioned temperatures.

The difference in rate of heat production between the male and the female of many species may be regarded as: (*a*) a genetic difference as fundamental as sex itself; or (*b*) a condition resulting from the differentiation and functioning of the gonads, that is, a secondary sex difference; or (*c*) the result of the two factors acting together or in succession. We do not yet know which of these alternatives is best supported by experimental data which indicate that anatomical differences between the sexes modify the production and loss of heat. To quote from Deighton:[26]

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[19] Mitchell, H. H., and W. T. Haines, Jour. Agric. Res., 1927, vol. 34, p. 927.

[20] Mitchell, H. H., L. E. Card, and W. T. Haines, Jour. Agric. Res., 1927, vol. 34, p. 945.

[21] Herzog, D., Wissensch. Arch. f. Landwirtsch., 1930, vol. 3, p. 601.

[22] Benedict, F. G., W. Landauer, and E. L. Fox, Storrs Agric. Exper. Sta. Bull. 177, 1932, p. 13.

[23] Brody, S., E. M. Funk, and H. L. Kempster, Missouri Agric. Exper. Sta. Res. Bull. 166, 1932, p. 67.

[24] Riddle, O., G. Christman, and F. G. Benedict, Amer. Jour. Physiol., 1930, vol. 95, p. 111.

[25] Riddle, O., G. C. Smith, and F. G. Benedict, Amer. Jour. Physiol., 1932, vol. 101, p. 260.

> Bohnenkamp and Pasquay[27] Mitt. V, give weighty reasons for thinking that the well-known difference in basal metabolism between males and females of many different species, including man, depend in the first place on skin temperature difference due to greater thickness of subcutaneous fat in the female. This extra fat lowers the specific gravity, that of women being found to be distinctly less than that of men. Arguing from this they are able to account satisfactorily for (*a*) the fall of basal metabolism with age, and (*b*) the greater approximation of the sexes in this regard as age advances. It seems also to explain the greater ability of women as swimmers and certain peculiarities of the metabolism of pachyderms and cetacea. One noteworthy point is that the reduction in skin temperature due to fat, in a fat man, actually makes a greater difference in the metabolism in a negative direction than does the consequent areal increase in a positive direction.

The above statement does not apply to doves and pigeons.

Results Obtained from Doves and Pigeons

Fully tabulated data (tables 14–64) for the sexes could be expected, particularly in the case of ring doves, to provide a definite answer to the question of the relation of sex to heat production. Our own study of this large body of data leads to the conclusion that the results demonstrate that the metabolism of male ring doves suffers a greater decrease with increase of external temperature (from 20° to 30° C.) than does that of females. Relative rates of heat production at the various temperatures by the two sexes were not determined in a completely satisfactory manner. The tabulated data require a series of corrections, most of which are not yet well evaluated. The sex difference in the momentary rate of heat production of adult doves is slight, and it probably varies among the races used in this study.

It does not seem probable that any individual race or type provides as accurate a measure of the influence of the sex factor as does a group of types; this inference, of course, is based on the assumption that the several members of the group are measured with acceptable adequacy and accuracy. For this reason the following discussion of present results for ring doves is based chiefly on data (obtained at 30°, 20°, and 15° C.) from adults (not old, not young) belonging to 35 types (24 types at 15°). Excluded from this group are data from (*a*) "miscellaneous" races and hybrids, (*b*) types in which the "yearly average" was obviously unbalanced by absence of data for a season, and (*c*) any set of measurements (for the two sexes at a particular temperature) not based on more than 24 individual determinations. Thus, at 15° C. 11 of the 35 types were excluded, although these types are represented in measurements made at 30° and 20° C. In all comparisons made between values obtained at 30° and at 20° the same 35 types are involved.

The group of dove types described above yielded the following average calories per kilogram per hour: At 30°, males 4.60 ± 0.038; females 4.88 ± 0.044. At 20°, males 6.24 ± 0.052; females 6.30 ± 0.066. At 15°, males 7.24 ± 0.081; females 7.30 ± 0.071. Standard errors of the means are given, though they actually relate to the variability of "racial" differences rather more than to sex difference in heat production within a race. It may be noted that in only 3 of the 35 types did the metabolism of males exceed that of females in tests made at 30° C.; these 3 types also showed higher values for males at 20°; and, though only 1 of the 3 was adequately measured at 15°, this value for males also exceeded that for the females of the type. Thus, in 3 racial types the males yielded consistent evidence of a slightly higher rate of heat production than that of females of their type. In measurements made at 20° the males of 15 of the 35 types had the higher metabolic rate; at 15° the males of 10 of the 24 types had a higher metabolic rate than that of the corresponding females. These several comparisons are based on the uncorrected tabulated values; all values assigned to females in the tables are too high, since, in general, they are subject to reductions which will be noted below.

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[26] Deighton, T., Physiol. Reviews, 1933, vol. 13, p. 427.

[27] Bohnenkamp, H., *et al.,* Pflügers Arch., 1931, vol. 228, p. 40.

It will be observed that at 30° the average metabolism of the males in the above-mentioned group is 5.7 per cent less than that of the females; at 20° it is 0.95 per cent less; and at 15° it is 0.82 per cent less. In chapter 11 it was shown that the nonmetabolizing plumage of male doves exceeds that of females by 0.6 per cent; this value (0.6 per cent) should be subtracted from the percentages given immediately above, since the metabolism values were calculated directly from body weight. The extent to which the average metabolism of the female doves was influenced by the inclusion of birds measured at a special stage of the reproductive cycle (within 50 hours of ovulation) should next be considered. Thereafter, it will be necessary to discuss the significance of slightly unequal body size, the unequal effect of high temperatures on the 30° metabolism of male and female doves, and the indirect effect of extra insulation (plumage) on the heat production of males.

Before considering our own measurements which were designed to determine in doves the effect of proximity to ovulation, it seems well to review the results of comparable tests made on other species. Gerhartz[28] observed that the basal heat production of 2 hens was much higher during the laying season than at its end. Other investigators[29,30] reported inconclusive results from relatively few tests. Dukes[31] found that the basal metabolism of 8 hens was higher just before and during periods of laying than when they were not laying; in 5 of these the increase amounted to 10 per cent or more (17 and 37 per cent in 2 hens). The average rate for the 10 hens measured during laying periods, or within 6 days prior to laying, was 10 per cent greater than for 8 nonlaying hens. A 2-year study of the domestic fowl during the pullet stage was made by Winchester,[32] who con

[28] Gerhartz, H., Arch. f. d. ges. Physiol., 1914, vol. 156, p. 1.

[29] Mitchell, H. H., and W. T. Haines, Jour. Agric. Res., 1927, vol. 34, p. 927.

[30] Brody, S., W. M. Funk, and H. L. Kempster, Poultry Sci., 1932, vol. 11, p. 133.

[31] Dukes, H. H., Jour. Nutrition, 1937, vol. 14, p. 341.

[32] Winchester, C. F., Missouri Agric. Exper. Sta. Bull. 315, 1940, p. 1.

cluded that there was a parallelism between rate of egg production (grams per hen for 30 days) and basal heat production. Both were considerably higher during the winter and spring months, when the environmental temperatures (never lower than 2° C.) were mostly below the yearly average. Verzár and von Arvay[33] reported that the metabolism of rats at estrus was increased by fully 10 per cent by the marked increase in the size and motility of the uterus which occurred at that time; and von Arvay[34] observed an increase of 156 per cent in the oxygen consumption of excised uterine tissue of rodents previously injected with the sex hormone of the ovary. These several studies indicated that the temporary enlargement and motility of the oviducts and uteri of fowls and rats are associated with rather marked temporary increases in metabolic rate.

Tables 42 and 43 give results of our attempt to measure the influence of this factor in races of doves and pigeons. In all females which were measured within 50 hours of the ovulation of either a "first" or a "second" egg, the weight of the inert contents of the eggs, or of the yolk, was subtracted from the observed body weight before the heat production was calculated. Thus, that inert material, when present, did not enter into the calculations of any part of our tabulated data although body surface was increased in most cases. Too few pigeons were measured to provide reliable results, and perhaps the data obtained from them should be disregarded in the following discussion, which relates to ring doves. Data for hybrids, unless fully classified and compared with controls of their exact type, cannot be similarly tabulated and utilized because of possible effects of heterosis in the F_1. It will be seen that the metabolism of those doves which were within 50 hours of an ovulation period was apparently increased by about 1.6 per cent. Since, on the average, 1 of each 8 birds measured was in this reproductive stage, it is evident that the average values for females (as tabulated) should be reduced by 0.2 per cent in order to rule out effects of this particular stimulation. Again, probably as many as one-third of the females measured were only slightly more removed from ovulation, i.e., 50 to 125 hours; if this metabolic stimulus extends into that period—this is quite probable—a further marked reduction of the average values obtained for females is required. The correction for nearness to ovulation is underestimated. This correction, however, together with that for excess plumage weight of males, suffices to equalize the metabolism of male and female doves, when measurements are made at 20° or at 15°. At 30° the value obtained for females, even with these two corrections made in full, exceeds that of males by about 2 to 5 per cent. The basis, or meaning, of that excess will next be considered in detail.

Elsewhere (chapter 14) it has been shown that the data obtained in this study established the fact that the metabolism of male doves undergoes a greater change than does that of females when the two sexes are subjected to a particular range of temperature, namely, 20° to 30° C. There is no doubt that this result relates to sex and that it is well established. This fact, however, is open to various explanations. Two alternatives are, first, that the metabolism of males is more stimulated by 20° temperatures, and, second, that it is more depressed by 30° temperatures. It is also possible that the "critical temperature" of females is slightly below that of males, and that at 30° they are already showing an increased metabolism, as both sexes are known to do at 32-33° C. These and other considerations were discussed as follows in 1930 by Riddle, Christman, and Benedict:[35]

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[33] Verzár, F., and A. von Arvay, Biochem. Ztschr., 1931, vol. 240, p. 28.

[34] von Arvay, A., Endokrinologie, 1933, vol. 13, p. 9.

> The data would permit us to show specifically that the metabolism of certain races[36] is more affected by high temperature than is that of other races. Also that certain races are consistently characterized by an unusual body temperature (e.g., race *51*). . . . We conclude that many of the ring doves studied by us—taken at all seasons and previously subjected to a constant temperature of 30° C. (and motionless air) for 24 to 30 hours—are in a "non-physiological" condition. We do not say that they are pathological. But most of these animals (i.e., during most months of the year) are physiologically adjusted to a lower temperature and to a temperature which fluctuates slightly or considerably (and to moving air). We think of the 30° temperature as suddenly forcing a heavy burden upon the water regulatory mechanism at a time when the thyroid and other mechanisms for maintaining heat production (also quantity of food or energy intake) have not had sufficient time for their usual and normal abatement. Such a period of stress is markedly unusual and thus essentially abnormal; it can be considered physiological only in the sense that the organism's reaction against infection or invading disease is physiological—and both of these types of stress should be considered abnormal in a study of standard metabolism.
>
> We do not suggest that males only are put in a non-physiological condition by subjection to a temperature of 30°. Some females are undoubtedly affected. One female "scraggly" common pigeon—a defectively feathered race which uniformly shows a very high rate of heat production—is among the five birds which died apparently as a result, however indirect, of subjection to this temperature. We further and specially note that the "critical" temperature for females may be slightly lower than that for males—and slightly lower for both sexes in some races and at some seasons than in others. In a recent and important paper dealing with experiments on the adaptation of rats to air of reduced cooling power Sundstroem[37] finds that the "rats suffered a great deal from discomfort" during their first days in such a climate. Moreover, he obtained indications that female rats show less mortality than do males when both are exposed to air of low cooling power.

In a later publication Riddle, Smith, and Benedict[38] noted reasons for believing that measurements made on Tippler pigeons at 20° provided a truer measure of the seasonal factor than did measurements made at either 15° or 30° C. It is the writer's opinion that this same statement applies also to the sex factor.

Two items concerning the relation of sex to metabolism in ring doves remain for consideration. The body weight of males exceeds that of females (see chapter

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[35] See footnote 24.

[36] See chapter 13.

[37] Sundstroem, E. S., Univ. California Publ., Physiol., 1930, vol. 7, p. 103.

[38] Riddle, O., G. C. Smith, and F. G. Benedict, Amer. Jour. Physiol., 1934, vol. 107, p. 333.

2), and a proper correction for this factor would tend to increase the heat-production values for males in relation to those for females. The extent of that increase is uncertain, but when combined with the corrections made previously it would clearly suffice to render the average values for males measured at 15° and 20° slightly higher than those for females, and it would reduce the 2–5 per cent excess otherwise shown by females measured at 30° C. The body weights of the males (groups of the various types at the end of measurements) exceeded those of corresponding females by values ranging between 0 and 13 gm. The average amount by which the body weights of these groups of males exceeded that of the females was 4 per cent. In this connection it should be observed that among the doves only races *N2* and *44* showed no sex difference in body weight. The metabolism of race *44* was not measured, but in race *N2* the heat production of males exceeded that of females (see table 26) at all temperatures, the percentage excess being 2.9 at 30°, 6.2 at 20°, and 5.1 at 15° C.

Finally, the influence on the adult male metabolism of the greater insulating powers of excess feather weight (over that of females) has not been considered; and indeed it is not determinable. If it were determined, there would perhaps still remain a question whether it represents something to be added to the observed values for males, or whether it should be regarded as an integral part of maleness. In the latter case, however, it should be noted that this difference could not apply to naked stages of the embryo; it could apply only to later life stages.

Again, turning from consideration of the mass data for the sex factor in doves, it is possible that the relation of metabolic rate to sex, in adult stages, is not invariable; that, as the uncorrected data suggest, metabolic rate during adult life is higher in the males of some races and higher in the females of other races.

For common pigeons the data which relate metabolism to sex are much less adequate than those for doves, but these data are not negligible. The following short discussion is based on data (obtained at 30°, 20°, and 15°) from adults (not old, not young) belonging to 10 types (5 types at 15°) for which more adequate data were obtained. Exclusions from this group were made on the same basis as in the case of ring doves in the comparable mass test. This group of pigeons yielded the following average calories per kilogram per hour: At 30°, males 3.90; females 4.12. At 20°, males 4.27; females 4.57. At 15°, males 4.79; females 4.96. In all the 10 types the females showed higher values than the corresponding males, both at 30° and at 20°. The heat production of the males was less by 5.5 per cent at 30°, 6.5 per cent at 20°, and 0.3 per cent at 15° than that of the females.

In general, 1.0 per cent is deductible from all the last-named values because that amount of excess plumage weight (nonmetabolizing material) is carried by the males. The small amount of data obtained for the effect of nearness to ovulation (table 43) in pigeons leaves it doubtful whether something should be subtracted or added for this factor. It should be noted that the heat production of male pigeons, unlike that of male doves, was not measurably depressed (relative to that of females) at a temperature of 30° C. The median weight of the dry skeleton of females, relative to their body weight, was 0.3 per cent greater than that of males. That amount (0.3 per cent) may properly be added to the percentages by which the heat production of females exceeds that of males. The body weights of the groups of male pigeons measured exceeded those of the females by amounts ranging from 4 to 47 gm. The only exception relates to Magpies, in which the average weight of the males measured was 292 gm. and that of the females 298 gm. In terms of percentage, the body weights of males (at the end of measurements) ranged from 2 per cent under to 13 per cent over the body weights of the females. The average of the male body weights exceeded that for the females by approximately 6 per cent. This is a notably greater sex difference than was observed in doves (4 per cent). A proper recognition of this difference in terms of surface area, if that were definitely attainable, would increase significantly the values obtained for males in relation to those for females.

The above summary does not include a consideration of the role of the insulating effect of the extra plumage carried by males. Although this excess is only 1.0 per cent in terms of body weight, it represents 11 per cent more of "heat-conserving" material, per unit of body weight, than was present on females. Irrespective of whether or not this excess of insulating covering in the adult male is properly assignable to maleness, it seems probable that it is responsible for a marked depression of the observed rate of heat production in adult males. In scraggly pigeons the insulating capacity of the plumage is partly lost, and in them the rate of heat production is greatly and consistently increased.

A total of 38 measurements were made to determine the effects of castration on heat production in Tippler pigeons. The results are presented in table 45. Three male castrates, measured at 30°, gave an average value 5.2 per cent less than that for normal males measured at the same season; and at 30° 2 female castrates gave values 16.2 per cent lower than their control. At 20° the "yearly average" heat production of 25 castrates exceeded that of their controls by 4.4 per cent; and at this same temperature the value obtained for 8 female castrates exceeded that for their controls by 1.7 per cent. These tests indicate that castration did not markedly affect metabolic rate in Tippler pigeons, and suggest that the nature of the effect may vary according to the temperature at which the measurements are made.

Ten measurements made on a hermaphrodite pigeon of race *267* (table 58) indicate a rate of heat production which, though apparently slightly reduced, is probably not significantly different from that of normal males of the same race.

Summary and Conclusions

The rate of heat production of male ring doves undergoes greater change than does that of females when the two sexes are subjected to a particular range of temperature, namely, 20° to 30° C. This difference was not noted in pigeons, but it was more definitely established than was any other sex difference in the heat production of ring doves.

In explanation of the above-mentioned difference, it is considered probable that males are more affected than females by maintenance at 30° in still air for 24 hours in preparation for the tests; and that, despite the fact that males yield lowest metabolism values when measured after 24 to 30 hours of such confinement, male doves are not then in a normal physiological state. It is also possible that female doves yield their lowest heat-production values at a temperature somewhat lower than 30° (perhaps at 28° or 29° C.).

Some females were measured close to the time (within 50 hours) at which they would ovulate an egg; at this time the oviduct is unusually large and presumably in active movement. Measurements were made on birds of pure races to determine the extent to which these temporary conditions affect the metabolic rate. An inadequate number of such measurements were made on pigeons. The measurements made on doves show that these conditions were associated with an increase of nearly 2 per cent in heat production. The actual increase over the period of complete reproductive rest is probably considerably greater.

Relative male and female rates of heat production at temperatures of 30°, 20°, and 15° cannot be given with accuracy. All the tabulated values (calculated as calories per kilogram per hour) require at least slight corrections for the smaller plumage weight of females, for the stimulus of a special reproductive stage in a fraction of the females, and for the smaller average body weight of females (4 per cent less than in males). The above corrections would apparently result in slightly higher values for heat production in the males of most dove races or types measured at 20° and 15°. Perhaps the reverse result would still be indicated by most measurements made at 30° C. The data obtained do not exclude the possibility that, in adult doves, the relation of "basal" metabolic rate to sex is variable, with a higher rate in males than in females in some races and a lower rate in others.

It is the opinion of the writer that in doves and pigeons the influence of the sex factor on heat production is better shown by measurements made at temperatures around 18°–24° than at the "critical" temperature (30° C.); and that the optimum temperature itself varies according to season.

The influence on metabolism of the greater heat-insulating powers of excess feather weight in adult males (over that of females) is probably large, though it has not been measured. It is pointed out that this difference cannot exist in embryos at the naked stage.

Significant though less adequate data obtained for the two sexes in pigeons are subject to the several corrections indicated above for doves. Those corrections would result in values which, in general, would indicate an equal or higher rate of heat production in males measured at 15°; at 20° and 30° an opposite slight sex difference would be indicated. Again, these several results must be viewed in the light of the fact that adult male pigeons have approximately 11 per cent more heat-insulating material (plumage) than do females.

The data obtained for adult pigeons do not exclude the possibility that the relation of metabolic rate to sex is variable; possibly the adult males of some races have a higher, others a lower, rate of heat production at all temperatures of measurement than do the associated females.

A prolonged and careful study of the relation of metabolism to the sex factor—somewhat subordinated, it is true, to the race factor—has indicated several complications which attend attempts to resolve this problem in doves and pigeons. It has been shown that, in general, no more than a slight sex difference in rate of heat production exists in adults of breeds and races of these two species.

Thirty-eight measurements made on castrate Tipplers of both sexes indicated that castration did not markedly affect their metabolic rate; the results suggest that the nature of the effect may vary according to the temperature at which the measurements are made.

16

ORGANS HAVING SPECIAL RELATIONS TO HEAT PRODUCTION

When the present study was initiated it was assumed that marked differences in rate of heat production in the various dove races would relate chiefly, at least, to differences in level of thyroid functioning. Several facts accumulated during the intervening years largely support that assumption. On the other hand, one group of studies has shown that the thyroid itself is largely under the control of the anterior pituitary; another group of studies has been interpreted to indicate a special influence by still other organs, such as the brain and adrenals, on heat production; finally, our own laboratory has shown that prolactin increases the heat production of normal doves and pigeons, and of pigeons from which either the pituitary, the thyroids, or the adrenals have been removed. In this connection it may be noted that in pigeons prolactin has special ability to support growth in the intestine, liver, and pancreas. The constitutional factors chiefly concerned in heat production therefore require the review and discussion accorded them in the following pages.

General Considerations

The size of the brain is considered by Kestner[1] to be the chief factor in conditioning the intensity of basal metabolism, because of the high oxygen requirement of this organ. Young animals have relatively much larger brains than adults, and small animals have relatively heavier brains than animals of larger species. The postnatal growth of the brain, in several species of mammals, was found to be distinctly slower than that of the body; that of the liver, heart, and kidney was also somewhat slower (as the ⅔ power of the body weight). Muscle, however, increased more rapidly than body weight. The oxygen consumption of the brain is known to be considerable. Kestner concluded that the relative size of the brains and large glands can account for the intensity of metabolism in different animals.

Crile[2] regards the neuro-endocrine system as exercising an energy-stimulating action upon the organs of the body. His views differ from those of Kestner in that he assigns to the brain a primary conditioning function in basal metabolism. He refers to the brain as the "universal executive of energy," to the role of the thyroid gland as that of maintaining the level of constant activity in the controllers of oxidation, and to the role of the adrenal glands as that of promoting oxidation for energy needed in emergency. Crile and Quiring claim to have demonstrated a constant relation between the size of an animal's brain and its metabolism. It is stated that 1 gm. of brain is required to release 12.115 calories of heat in 24 hours. Their conclusions are based on the study[2] of a large collection of organ weights from 3694 animals: among these were tropical and northern species of rodents, carnivores, and ungulates; domestic animals, including different types of horses; also, three species of cetaceans. Using the relative growth equation, the degree of brain development was found to be greater in the subarctic rodents, carnivores, and ungulates than in tropical representatives. The thyroid gland showed a larger coefficient of growth in the subarctic rodents and carnivores than in the tropical ones. The heart likewise showed a greater relative weight in subarctic forms, especially in the carnivores and ungulates. The adrenal coefficient was larger in subarctic rodents, smaller in subarctic carnivores (but the latter included some aquatic species). In the white whale the brain and thyroid gland showed much larger relative weights than in any of the nonaquatic mammals, the brain coefficient being 3 times greater than that of the largest ungulates studied. This condition was attributed to excessive heat loss by the whale in cold arctic waters, resulting in stimulation of metabolism.

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[1] Kestner, O., Jour. Physiol. (Proc.), 1936, vol. 87, p. 39.

[2] Crile, G. W., Educ. Rec., 1941, vol. 22, suppt. 14, p. 57; Crile, G. W., and D. P. Quiring, Ohio Jour. Sci., 1940, vol. 40, p. 219.

A comparison of 154 horses of different types (including some burros, mules, and zebras) led to correlations between gland weights and type of ancestral environment (climate), exemplified by the small thyroids in Arabian horses, large ones in Shetland ponies. It was found also that the weights of the brain, heart, and thyroids, and the blood volume were correlated with the degree of activity in different breeds, and were highest in thoroughbred racing horses. These authors[3] compared the organs of a racing stallion, "Equipoise," with those of a white whale of the same weight. The whale's thyroid was found to be 3.23 times as large as that of the horse and the brain 2.9 times as large, presumably to maintain a high metabolism to compensate for rapid heat loss in cold water. The weight of the heart in the horse was 1.4 times, and that of the adrenal glands 1.3 times, greater than that in the whale.

Brody and Kibler[4] believe that the decline in the ratios of functional (metabolic) levels to body weight with increasing size reflects the decline in the ratio of the weight of "limiting" organs to body weight. "*A priori* considerations suggest that the ratio visceral-organ weight body weight should decline with increasing body weight, because from the principle of similitude, the ratio supporting structural (muscles and bones) body weight must increase with increasing weight." Starting with this hypothesis, they made an extensive analysis of published data on the relative growth of organs in various vertebrates, chiefly birds and mammals, and expressed their results in the form of charts. They compared mature individuals of different species, and also growing and mature animals of the same species. They found a close correspondence between the slopes of the curves relating the weights of neuro-endocrine systems to that of the body, and the slopes of curves relating metabolic levels to weight of the body. In both cases the values of the exponent b (in the relative-growth equation, $y = aX^b$) were considerably less than 1. Of the visceral organs, they emphasized the importance of the brain, the pituitary, adrenal, and thyroid glands, and the digestive system in limiting the resting metabolism in growing mammals and birds. The weight of the circulatory system, especially the heart and blood, tended to vary more directly with body weight (b more nearly 1). In mature animals of different species, the values of b relating visceral organ weights to body weights were found to be less than 1, but were somewhat higher than for the later stages of growth within a species. No data concerning weight of the brain were obtained in the present study.

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[3] Crile, G. W., and D. P. Quiring, Growth, 1940, vol. 4, p. 291.

[4] Brody, S., and H. H. Kibler, Missouri Agric. Exper. Sta. Res. Bull. 328, 1941.

Available data for pigeons permit an appraisal of the relative shares of the pituitary, the thyroids, and the adrenals in the stimulation of heat production in these particular birds. This laboratory has measured the effect of removal of each of the above-mentioned organs on the basal heat production of pigeons. At 10 to 20 days after complete hypophysectomy, the basal metabolic rate (B.M.R.) of adult pigeons showed a decrease of 33 per cent.[5] It is true that this operation (also adrenalectomy) decreased food consumption to about one-fourth of normal, and this decrease may have produced a part of the observed decrease in heat production. Two pituitary products, thyrotrophin and prolactin, are known, however, to increase the heat production of doves and pigeons measured at 30° C. (but not at 15° C.).[6] Removal of the adrenal glands from salt-maintained young pigeons produced little or no change directly due to loss of adrenal hormones.[7] At 6 to 46 days after removal of the thyroids from both young and adult pigeons a decrease of 27 per cent in the B.M.R. was observed.[8] Prolactin increased heat production in the absence of the pituitary,[6] thyroids,[6,9] and adrenals.[9] Though these data do not identify the source of the heat-producing effect of prolactin, they do make it clear that (*a*) the thyroid unquestionably plays a highly significant part in heat production, (*b*) the adrenal plays no more than a minor part (at least in short-term tests), and (*c*) much of pituitary action on heat production is exercised through the thyroid. Indeed, the effect of the thyroid is probably actually greater than could be observed in our tests, since Krause[10] reported traces of (nonremovable) sublingual thyroid tissues in pigeons. Those traces doubtless soon hypertrophy and function to an appreciable extent when all other thyroid tissue is removed.

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[5] Riddle, O., G. C. Smith, and C. S. Moran, Proc. Soc. Exper. Biol. and Med., 1935, vol. 32, p. 1614.

[6] Riddle, O., G. C. Smith, R. W. Bates, C. S. Moran, and E. L. Lahr, Endocrinology, 1936, vol. 20, p. 1.

[7] Riddle, O., G. C. Smith, and R. A. Miller, Amer. Jour. Physiol., 1944, vol. 141, p. 151.

[8] See data in paper of Marvin, H. N., and G. C. Smith, Endocrinology, 1943, vol. 32, p. 87.

[9] Riddle, O., and G. C. Smith, Proc. Soc. Exper. Biol. and Med., 1940, vol. 44, p. 499.

[10] Krause, R., Mikroskopische Anatomie der Wirbeltiere in Einzeldarstellungen, pt. 2, 1921 (W. de Gruyter & Co., Berlin and Leipzig).

Heart Weight and Metabolism

Historical

What is the relation, if any, between the size of the heart in animals and their metabolic activities? Does heart size exercise a limiting or conditioning effect upon metabolism during rest, or under conditions of physical stress? It has been pointed out by several investigators[11] [12] that the average increase in weight of the visceral organs as a whole, and of certain ones in particular, is more nearly proportional to the $^2/_3$ power of the body weight than to body weight as such. This fact corresponds closely to the increase in total metabolism in relation to the body weight of small and large individuals of the same or different species. The weight of the heart and blood, however, tend to vary more directly with body weight; that is, the exponent in the growth formula is nearer to 1.

There is little direct evidence of a correlation between heart size and basal metabolism per unit of surface in nearly related species. It is difficult to show such a relation even in widely differing species. In birds and mammals the relative heart weight (percentage of body weight) is in general somewhat less for larger species than for smaller ones; and for animals of the same species, of different size, this relation holds more perfectly.[13] This might be taken to indicate a direct relation between heart size and resting metabolism within a species, since the basal metabolic rate per unit of surface is known to decrease with increasing age in many species. With increase in size of the individual, however, the metabolic rate has been found to decrease in some cases (e.g., dog, cow, and steer) and to increase in others (cat, horse, bull).[14] Moreover, this direct relation between heart size and basal metabolism does not hold for the interspecific comparison, since the basal rate according to body surface is generally higher for larger species than for smaller ones.[14] In fact, if relative heart size were to decrease systematically from the small to the large species, it would correlate directly with the rate of metabolism per unit of body weight rather than per unit of surface.

It is probably true for the warm-blooded vertebrates—and especially for birds, in which heart weights exceeding 2 per cent of body weight are found[15]—that the large size of the heart is related functionally to their high resting metabolism as compared with that of cold-blooded animals. There are also reasons for thinking that in related species heart size is correlated with conditions which stimulate the activity metabolism or thermogenesis. Such factors as low temperature (cold climate, aquatic environment), high altitude, and degree of activity appear to influence relative heart weight through increased demands on the circulation.

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[11] Stewart, G. N., Amer. Jour. Physiol., 1921, vol. 58, p. 45.

[12] Brody, S., J. E. Comfort, and J. S. Matthews, Missouri Agric. Exper. Sta. Bull. 115, 1928. Also see footnote 4 above.

[13] Clark, A. J., Comparative physiology of the heart (Macmillan Co., New York, and Cambridge Univ. Press, 1927).

[14] Benedict, F. G., Vital energetics (Carnegie Inst. Wash. Pub. 503, 1938).

[15] Stieve, H., Zool. Anz., 1933, vol. 101, p. 233.

Joseph[16] found, in the various mammals which he studied, that the heart is relatively larger in the more active forms. This conclusion has since been confirmed by others. There is also some evidence which indicates that heart size is influenced by systematic exercise or rest in experimental animals. Some writers claim that the heart becomes enlarged in athletes after long-continued exercise, but this is denied by others. Hesse[17] made extensive observations on birds and mammals in different climates, living under natural conditions. He found that the relative heart weights of animals from a cool climate were greater than those of animals of the same or related species living in a warmer climate. Clark[18] has summarized the results of observations (up to 1927) dealing with the influence of mode of life, muscular activity, and climate on heart size. Included in his summary is a section on the relation of pulse rate and circulation volume to metabolism in different species.

The more recent investigations by Crile and Quiring[19-21] lend support to the above conclusions regarding the effect of activity and of climate on heart size. The experiments of Allee and Lutherman[22] should be mentioned as having a bearing on the influence of climate. They found that pullets which were reared at 6° C. from the third through the sixth month of life had significantly larger hearts than their former flockmates kept at 21° to 24.5° C. Strohl[23] called attention to the large size of the heart in a species of ptarmigan (*Lagopus*) living in the high Alps, as compared with the size in another species of the same genus living at lower altitude; his data indicated that heart size is influenced by altitude. Stieve,[24] however, after studying various species at different altitudes, concluded that there was no correlation between percentage heart weight and altitude.

Data for Doves and Pigeons

In the present study the relative heart weights, or percentage weights in terms of body weight, are given as median values for doves and pigeons of each sex, in figures 165 to 168. An attempt was made to show whether, in those races and hybrids for which there were adequate data, any relation exists between these percentage heart weights and the yearly average metabolism. There appears to be no consistent relation between heart weight and metabolism, even at 15°, a temperature at which muscle tone (activity?) might augment the metabolic rate and thus indirectly involve the heart. The values for percentage heart weight in the male doves (fig. 184) show a greater spread than do those for the females (fig. 185), and the values from males were therefore used in testing the degree of

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[16] Joseph, D. R., Jour. Exper. Med., 1908, vol. 10, p. 521.

[17] Hesse, R., Zool. Jahrb., Abt. f. allgem. Zool. u. Physiol., 1921, vol. 38, p. 243.

[18] See footnote 13.

[19] Quiring, D. P., Growth, 1938, vol. 2, p. 335.

[20] Crile, G. W., and D. P. Quiring, Growth, 1940, vol. 4, p. 291.

[21] Crile, G. W., Educ. Rec., 1941, vol. 22, suppt. 14, p. 57.

[22] Allee, W. C., and C. Z. Lutherman, Ecology, 1940, vol. 21, p. 29.

[23] Strohl, J., Zool. Jahrb., Abt. f. allgem. Zool. u. Physiol., 1911, vol. 30, p. 1.

[24] See footnote 15.

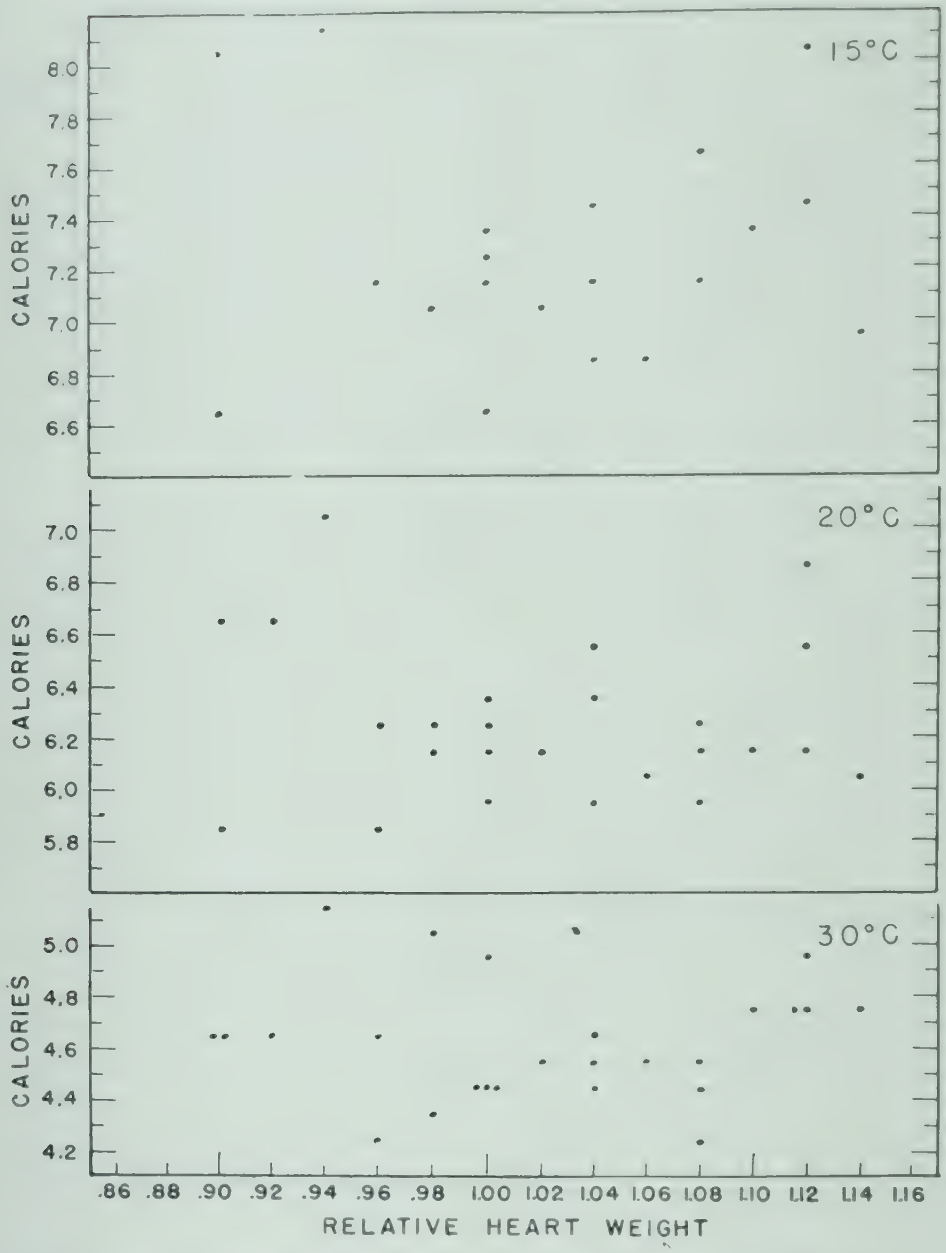

Fig. 184. Showing the relation of heart weight (as percentage of body weight) to fasting metabolism (calories per kilogram per hour) in male ring doves. Each point represents the yearly average metabolism plotted against the median heart weight of a race or type of hybrid.

correlation with metabolism. The coefficient of correlation for male doves was found to be +0.015 at 30°, −0.101 at 20°, and −0.008 at 15°. These results cannot be considered significant in view of the small number of cases, but may be taken to indicate the absence of any definite positive influence of heart weight on resting metabolism. In the female doves there is no apparent correlation between relative heart weight and metabolism at any given temperature.

In the case of pigeons, only the data obtained at 20° appear to be adequate for

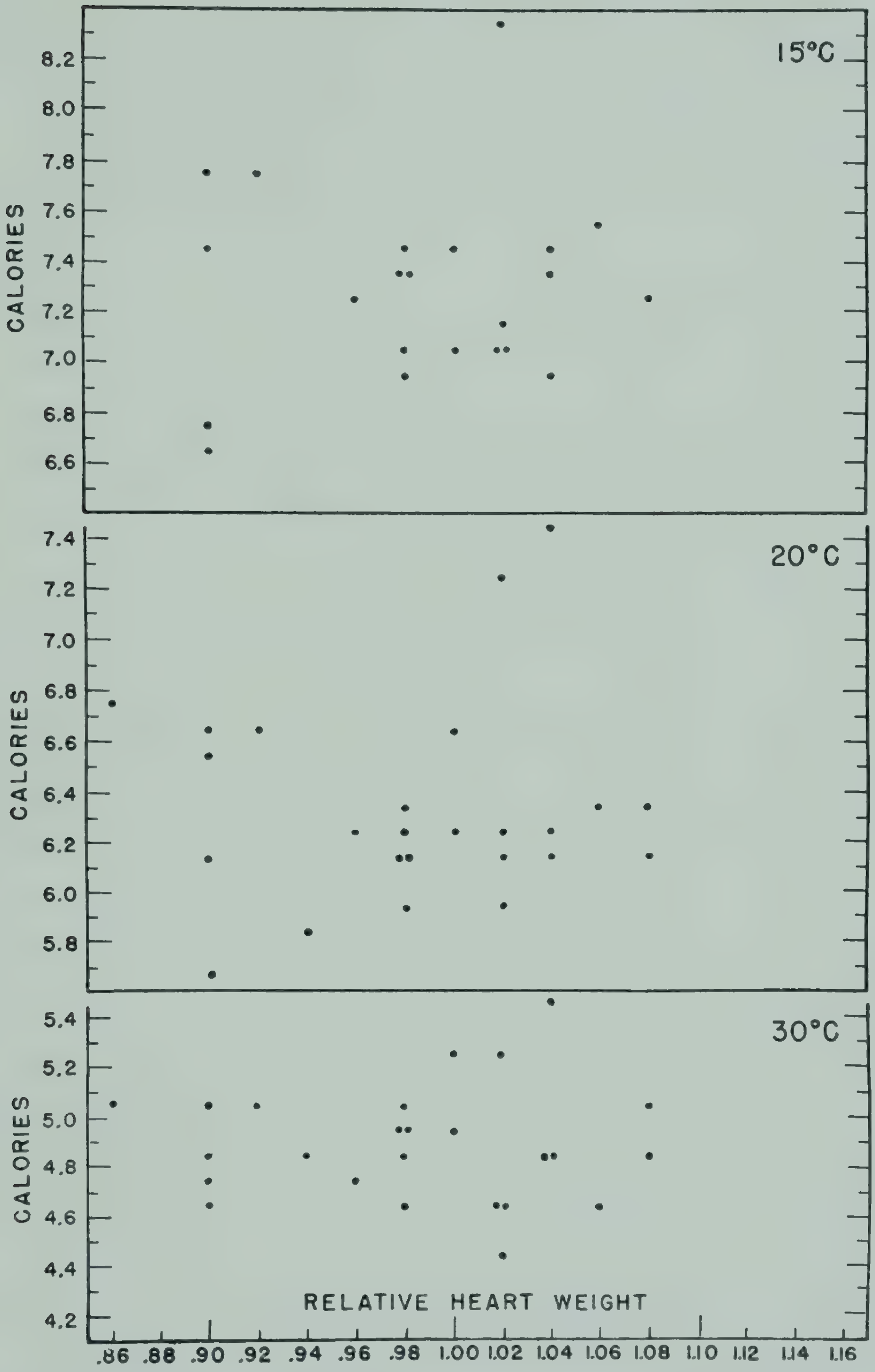

Fig. 185. Showing the relation of heart weight (as percentage of body weight) to fasting metabolism (calories per kilogram per hour) in female ring doves. Each point represents the yearly average metabolism plotted against the median heart weight of a race or type of hybrid.

testing the relation between heart size and metabolism. The body weight varies widely (from 277 to 598 gm.) in the various pigeon races and hybrids, and the percentage heart weights are somewhat greater in the smaller types studied than in the larger ones. Since metabolism per unit of body weight is in general greater in small birds than in large birds, one might expect to find a positive correlation between relative heart weight and metabolism in this group. Actually the coefficients of correlation for these 20° data are −0.069 for the males and +0.539 for the females.

Hemoglobin and Erythrocytes in Relation to Heat Production

The data of table 65 are not extensive but they show two interesting results. It has been observed that the rate of heat production in scraggly pigeons is much higher than that in any other type of pigeon, and therefore much higher than that in the two types (ataxic and normal) which apparently differ from it only in respect to the scraggly and ataxic genes. The blood of these three types, however, contains essentially equivalent amounts of hemoglobin. Complete examination of the data indicates that the slight apparent excess of hemoglobin in the ataxics is ascribable to the fact that a higher proportion of ataxic birds were tested in winter, the season of highest hemoglobin values. A second notable result is found in the fact that the blood of scragglies had a significantly lower red-cell count (particularly in males) than was found in the two related types.

TABLE 65

Average concentration of hemoglobin (grams per 100 ml. blood) and number of erythrocytes (thousands) in three types of SA-E pigeons
(predominantly summer values)

Kind of pigeon	Males				Females			
	No. of birds	Hemoglobin	No. of birds	Erythrocytes	No. of birds	Hemoglobin	No. of birds	Erythrocytes
Normal	16	16.70	19	3407	7	15.58	8	3348
Ataxic	11	17.27	24	3456	10	16.11	23	3355
Scraggly	12	16.80	17	3058	17	15.90	23	3307

It was earlier shown by Riddle and Braucher[25] that in both doves and pigeons, as these were maintained in our colony, hemoglobin values tended to be highest in winter and lowest in summer; erythrocytes were most numerous in autumn and fewest in summer. That study also provided evidence (*a*) that the mean annual concentration of hemoglobin is about 7.8 per cent, and the erythrocyte number 4.7 per cent, greater in pigeons than in doves, (*b*) that both hemoglobin and erythrocyte values for males exceed those for females, (*c*) that both values are slightly greater in young than in adult birds, (*d*) that close confinement (in space of 1 cu. ft.) for 1 month increases the cell count of ring doves, and (*e*) that dove and pigeon races have hemoglobin and erythrocyte values which, it can now be seen, are not associated in any regular way with their metabolic rates.

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[25] Riddle, O., and P. F. Braucher, Amer. Jour. Physiol., 1934, vol. 108, p. 554.

Both present and earlier data, therefore, indicate that in pigeons and doves the oxygen carriers of the blood are not reliable indices of the metabolic rates of racial types.

The Relation of Metabolism to Feather Development in Birds

The functional role of the feathers of birds, as a protective covering against the loss of heat from the body, has received but little attention from biologists. The relative importance of the weight and the number of feathers is the only aspect of the subject which has been investigated to any great extent with normal birds. Other conditions of the plumage which may play a part in temperature regulation are the length and width of the feather, in contrast with the size of the shaft (or quill), which largely determines its weight; the relative importance of different types of feathers; the elevation of the feathers in relation to the conservation and loss of heat from the body; and seasonal conditions of molting.

Historical

Some measurements of heat production were reported for a race of pigeons called "scraggly,"[26] and for "Frizzle" fowl,[27,28] both of which represent genetic strains characterized by abnormal types of plumage. In both these cases the birds had visibly defective feathers and an abnormally high rate of heat production; the latter compensated for an unusually high rate of heat loss.

In Single Comb White Leghorn fowl Latimer[29,30] found that the feathers form a larger percentage of the body weight in the adult than they do in the newly hatched chick. Their maximal relative weight, about 9.8 per cent, is reached slightly before half of the ultimate body weight has been attained (just before sexual maturity). Thereafter the relative weight of the feathers declined to 5.5 per cent in males and to 4.0 per cent in females. This sex difference (1.5 per cent of the body weight) in the plumage of adult fowl is greater than, but otherwise similar to, the average difference observed (part I) in adults of certain races of pigeons (1.0 per cent).

According to Hutt and Ball,[31] the number of contour feathers in birds of the order Passiformes (Wetmore's data[32]) increases in proportion to the 0.185 power of the body weight. The relatively greater number of feathers per unit body weight in small birds than in large birds is regarded as an adaptation for retention of heat, which is produced in larger amounts per unit of weight by small birds.

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[26] Benedict, F. G., Bull. Soc. sci. d'hygiène alimentaire, 1929, vol. 17, p. 321. (Data used were early results of Benedict and Riddle.)

[27] Benedict, F. G., W. Landauer, and E. L. Fox, Storrs Agric. Exper. Sta. Bull. 177, 1932.

[28] Landauer, W., Biol. Symposia, 1942, vol. 6, p. 127.

[29] Latimer, H. B., Jour. Agric. Res., 1924, vol. 29, p. 363.

[30] Latimer, H. B., Bull. Univ. Kansas, 1932, vol. 33, p. 199.

[31] Hutt, F. B., and L. Ball, Auk, 1938, vol. 55, p. 651.

[32] Wetmore, A., Auk, 1936, vol. 53, p. 159.

Brody and Campbell[33] estimated that in immature domestic fowls, when body weight increases 100 per cent, feather weight increases by 90 to 100 per cent and feather number by only 11 to 17 per cent. They concluded that, since neither feather weight nor feather number increases in proportion to the surface area of the body, probably neither factor is a satisfactory index of the insulating or thermoregulatory capacity of feathers.

Turner[34] found that the maximum weight of the plumage in cockerels was attained in 33 to 37 weeks after hatching. Jaap and Turner[35] made a study of the weight and number of feathers in relation to body weight; they also investigated the average weight of a feather and the dimensions of specific feathers in males of several breeds of fowl of different sizes. They were able to demonstrate breed differences, for example in length and width of specific feathers, in strains of Cornish and Rhode Island Reds. The average weight of a feather in White Wyandottes was distinctly greater than in either Dark Cornish Bantams or the Dark Cornish, a breed of similar body size. The feather weight per unit of body weight was slightly greater in the larger birds, whereas feather number per unit body weight was much greater in the smaller birds of the various breeds studied.

Data for Doves and Pigeons

For purposes of the present investigation some measurements were made of the total weight of the feathers in pigeons of 4 races and 2 hybrid groups, and 12 individuals of different races and hybrids (miscellaneous group); also, in doves of 8 races and 45 individuals of various other strains (miscellaneous group). From these data the percentage weights in terms of body weight were calculated and the results plotted (fig. 172). When the relative or percentage weight of the feathers for the pigeons and doves is compared, it is seen that the difference is rather small, in view of the considerable difference in their body weights. For the adults, of both sexes combined, the average feather weight for pigeons is 8.4 per cent, and for doves 7.7 per cent; for young pigeons it is 7.7 per cent, and for young doves 7.4 per cent.

In any attempt to show whether a correlation exists between the relative weight of the feathers in different pigeon races and their rates of heat production, differences in size of the races must be taken into account. For three of the races of pigeons used in this study, Tippler, Magpie, and *S.A-E.*, the average body weights (both sexes) were found to be 274, 320, and 342 gm., respectively, whereas the average weight of Runts was 560 gm. In the last-named race the lower basal rate of heat production per unit of weight (tables 3, 44) is doubtless associated with its relatively greater body size. The body weights of the pigeon hybrids studied averaged 440 gm. (Runt × Magpie) and 324 gm. (Magpie × *S.A-E*).

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[33] Brody, S., and J. Campbell, Missouri Agric. Exper. Sta. Res. Bull. 287, 1938.

[34] Turner, K. B., Proc. Oklahoma Acad. Sci., 1941, vol. 21, p. 93.

[35] Jaap, R. G., and K. Turner, U. S. Egg and Poultry Man., 1943, vol. 49, pp. 74, 90.

A comparison was made of basal heat production (at 30°) in the 4 above-named races and in Magpie × Runt hybrids; average heat production for the four seasons was used whenever this was available, and values for the two sexes were combined. Likewise, the *increases* in rate at 20° and 15° above that at 30° were compared. In some cases data were not available for all seasons. Thus, for Magpies at 30°, the data are for three seasons only, and for *SA-E* females at 15° the data are for winter and spring only. The basal rate of heat production (at 30°) per kilogram of body weight is approximately the same for the three races of similar size, ranging from 4.14 calories per hour in *SA-E* to 4.30 in Magpies (three seasons only); it is about 15 per cent lower in Runts. The difference in relative feather weight between *SA-E* (9.1 per cent) and Magpies (7.1 per cent) is 2.0 per cent, and since this represents a difference in weight of "nonmetabolizing" material, it would reduce to 1.8 per cent the observed 3.8 per cent difference in the metabolism of these two races.

The greatest increase in heat production at 15° over that at 30° (fig. 186) was

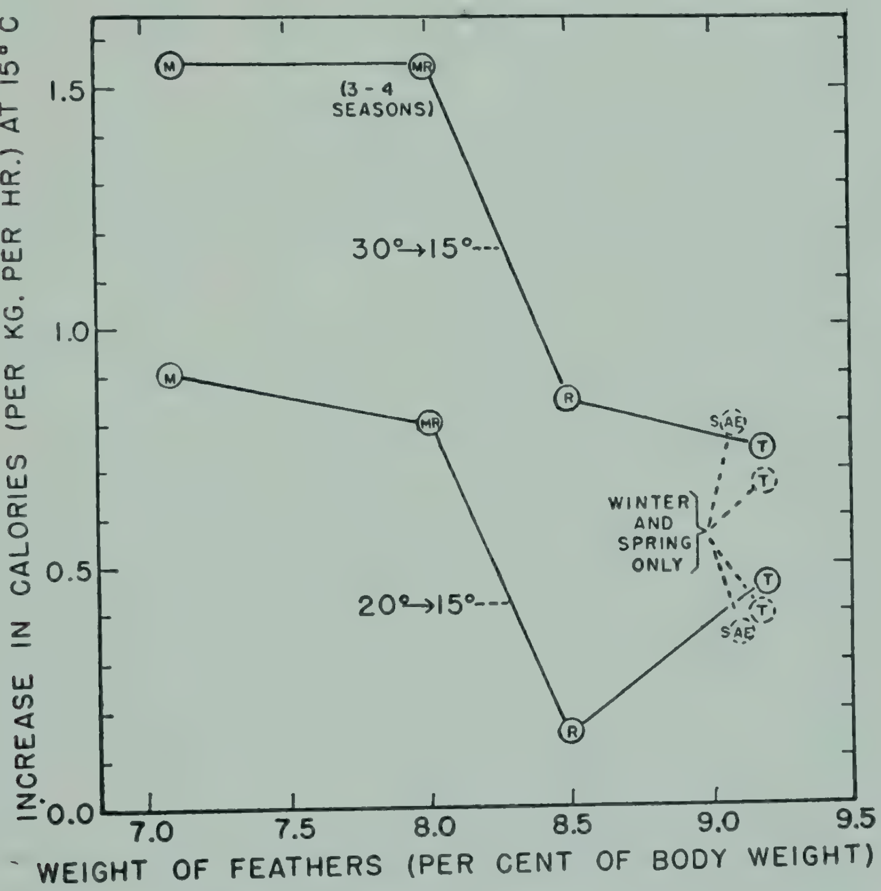

FIG. 186. Influence of low temperature on the metabolism of pigeon races Magpie (*M*), Runt (*R*), *SA-E*, and Tippler (*T*), and of a hybrid, Magpie × Runt. Showing the increase in heat production (calories per kilogram per hour) at 15° over the rates at 30° and at 20°. The figures for increased heat production are plotted against those for feather weight as percentages of body weight.

1.56 calories; this was observed in Magpies, the race with the lowest percentage of feather weight. The smallest increase (0.74 calorie) occurred in Tipplers, and this is the race with relatively heaviest (9.2 per cent) plumage. For *SA-E*, whose plumage weight almost equaled that of Tipplers, the increase of 0.79 calorie (winter and spring data only) is not much greater than the corresponding increase in Tipplers at the same seasons. In Runts, whose feather weight had an intermediate value of 8.5 per cent, the increase amounts to 0.84 calorie. In Magpie × Runt hybrids, feather weight 8.0 per cent, the actual values for 30° and 20° metabolism lie between those for the parent races at these temperatures. The increases in heat production by these hybrids (fig. 186) when the temperature was lowered from 20° to 15° and from 30° to 15° were nearly as great as in Magpies. Plumage weights of Magpie × Tippler hybrids were not obtained, but it is interesting to note that the metabolism of these birds was essentially intermediate to the values for the parent races at the three temperatures studied. In these hybrids, heat production at 15° increased over that at 20° almost as much as it did in Magpies, and in comparison with the 30° value it increased slightly more than in Magpies. Plumage weight in Magpie × *SA-E* hybrids was 8.4 per cent of body weight; this value is close to the average of the values for the two parental races. The heat production of this hybrid was inadequately measured.

When the basal metabolism of the 4 above-named races and the 1 type of hybrid is calculated according to body surface ($S = 10 \times W^{\frac{2}{3}}$) the following figures are obtained: for Magpies, 29.5 (3 seasons only); for Magpie × Runt, 28.3 (3 seasons only); for Runts, 28.6; *SA-E*, 27.6; and for Tipplers, 26.9 calories per square meter per hour. In general, the basal rate is thus seen to be inversely proportional to the percentage weight of the feathers; and the method used to obtain this result should largely eliminate inequalities due to differences in body weight.

A comparison was also made of the rate of heat production in 8 races of ring doves in relation to their relative (percentage) feather weight. Unlike the condition in pigeons, there is but little difference in the body weight of the dove races, so that a reliable comparison of their metabolism per unit of weight seems possible. The figures (medians) for feather weight range from 6.95 to 8.75 per cent for these particular types of doves. The values for average heat production for both sexes at 30° lie between 4.38 and 5.14 calories per kilogram per hour. When these figures are plotted against those for percentage feather weight there seems to be, at 30°, a small negative correlation (actually −0.3 by Spearman's formula), that is, a decrease in metabolism with increase in feather weight. At 20° the correlation coefficient is −0.1, and at 15° it is +0.4. This apparent trend toward a positive correlation as temperature is lowered is also shown when the increase in calories produced at 15° over 30° is plotted (fig. 187); here, by the same method of calculation, the coefficient is +0.4. In the 4 (of 8) races of doves having the highest percentage weight of feathers the average basal rate of heat production was 4.73 calories, and in the 4 others this value was 4.81 calories per kilogram per hour; these values involve a difference of 1.7 per cent in the metabolism, and this is associated with an average difference of 1.1 per cent in feather weight.

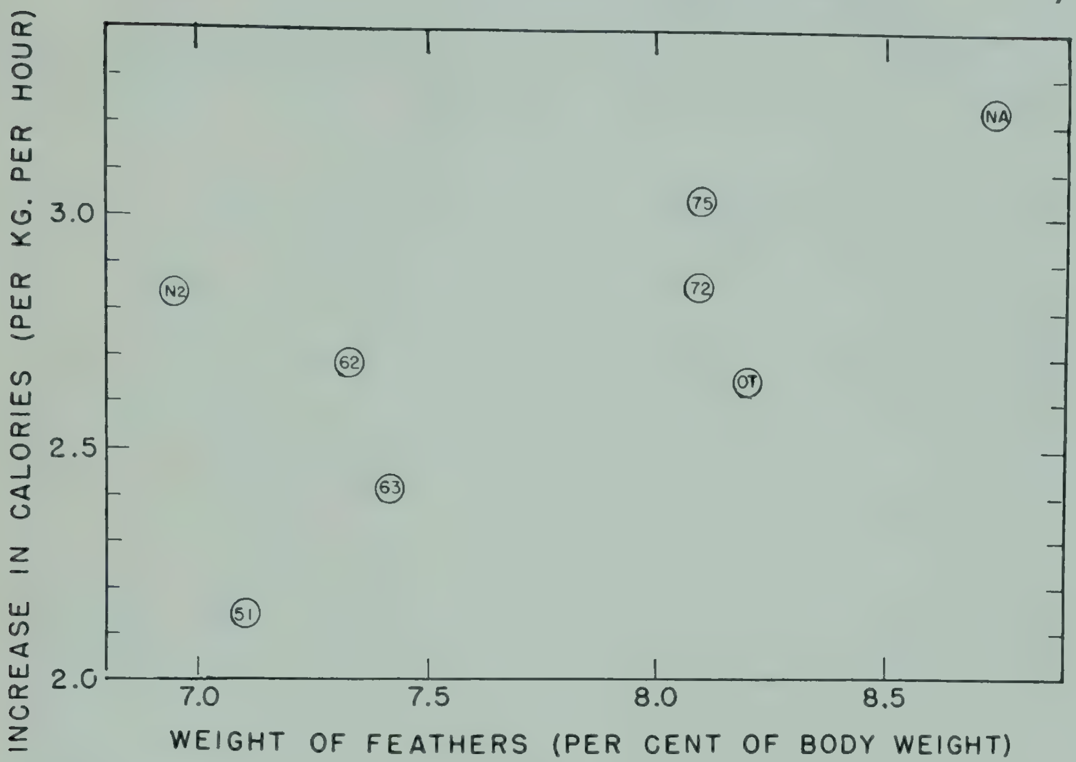

Fig. 187. Influence of low temperature on the metabolism of 8 ring dove races. Showing the increase in heat production (calories per kilogram per hour) at 15° over the rate at 30°. The figures for increased heat production are plotted against those for feather weight as percentage of body weight.

In conclusion, it may be said of the few pigeon races for which data on plumage were available that the values for rate of heat production at 30° suggest that the basal rate is influenced by differences in the relative weight of the feathers. The more reliable results obtained on ring doves give some indication that in these types also the basal metabolism is lower in birds with heavier plumage. To a considerable extent this condition can be accounted for by the difference in weight of feathers, regarded as inert material, but to an unknown extent it may be associated with unequal rates of heat loss incident to unequal plumage weights. The greater rise in heat production at low temperatures in Magpie pigeons than in other races may be related to the lower percentage weight of feathers in this race; but in 2 types of Magpie hybrids ($M \times T$ and $M \times R$) in which feather weight is known to be greater than in Magpies, the increase in heat production is of about the same magnitude as in Magpies, a fact which suggests that genetic factors other than those which affect the nature and amount of the plumage may affect metabolic rate. On the other hand, in ring doves there was a greater relative rise in rate of heat production at 15° over that at 30° in races with heavier plumage; this fact is difficult to account for, if the extra metabolism in response to cold is controlled by diverse rates of heat loss due to differences in feather weight. Perhaps this greater relative increase in heat production at a low temperature in doves with heavier plumage may be taken to indicate a greater power of active regulation of heat production or elimination on the part of these birds—presumably for the same reason that this ability is greater in women than in men (see chapter 15).

The Influence of Metabolically Inert Material

The weight of the nonmetabolizing tissues (skeleton, feathers, etc.) of the body is usually not taken into account in calculating metabolic rate. It may properly be considered in any attempt to explain small metabolic differences—such as those associated with age, sex, and race—among individuals whose differences in body weight are not significant. Moreover, since some investigators have attempted to explain the proportionality between metabolism and body surface area in terms of differences in protoplasmic mass, measurements of the amount of inert materials in species or races of different size should prove useful.

It is now generally recognized that the metabolically active tissues of the body increase almost in proportion to body weight and not to surface area. Terroine[36] found also, on the basis of analysis of the nitrogen content of birds and mammals, that protoplasmic mass is more closely related to body weight than to surface. Benedict,[37] who was one of the early advocates of the significance of protoplasmic mass, recognized this last-mentioned fact; he also emphasized the view that, in addition to active tissue, the "stimulus to metabolic activity"—perhaps greater in small animals than in large—was equally important.

In the following paragraphs feathers and skeleton are specifically considered. The whole of the fresh skeleton cannot properly be regarded as metabolically inert material. For purposes of the present study, the amount of dry matter obtained in skeletons is assumed to represent the amount of inert tissue.

The influence of feathers, considered as inert material, on the rate of metabolism of these doves and pigeons cannot be very great as compared with the considerable differences in rate found (especially among ring doves) for particular racial types. This racial difference, as already noted, amounts to 10 to 17 per cent. The extreme difference in feather weight (see chapter 11) in the 8 types of doves measured is 1.8 per cent, and that observed in 6 types of pigeons is 2.1 per cent of body weight; these differences should give rise to equivalent percentage differences in metabolism (per unit weight). Illustrations of the way in which a difference in weight of feathers, treated as inert material, would affect metabolism in pigeons and doves are given in the preceding section. The fact that additional feather weight presumably restricts heat loss, and may modify thermogenesis at low temperatures, was noted. It is evident, however, that the observed racial differences in basal heat production are only partly accounted for by plumage, either as inert or as heat-insulating material.

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[36] Terroine, E. F., and E. Zunz, Le métabolisme de base (Presses Universitaires de France, Paris, 1925).

[37] Benedict, F. G., and G. MacLeod, Jour. Nutrition, 1929, vol. 1, p. 343; Benedict, F. G., Vital energetics, p. 196 (Carnegie Inst. Wash. Pub. 503, 1938).

Feather-weight differences between the sexes are also large enough to account for measurable differences in metabolism. The plumage of female pigeons weighs 1.0 per cent less than that of males; if the plumage is considered as "nonmetabolizing" material, this difference requires a 1.0 per cent reduction in the metabolism (as now calculated) of females in order to make the values comparable with those of males. In ring doves the males have an apparent excess of plumage weight of only 0.6 per cent, and their values for heat production thus require an upward revision to the extent of 0.6 per cent.

The average weight of plumage of young pigeons is 1.0 per cent less than that of adult pigeons. For young doves there is considerable variability in the results (chapter 11), but their average plumage weight is 0.4 per cent less than that of adults. These percentages represent the amounts by which the calculated metabolism of young pigeons and doves should be reduced—for feathers considered as inert material—when comparisons are made with the metabolism of adults.

The unmeasured, but possibly marked, effect of excess plumage weight on heat production, through a greater restriction of heat loss, is not considered in the above statements concerning sex and age.

The dry weight of the skeleton, or at least a large proportion of it, can properly be regarded as inert or "nonmetabolizing" material in the calculation of heat production. The metabolism of the pigeons is roughly one-fourth less per unit weight than that of the ring doves. The dry weight of the skeleton in pigeons is about 4.0 per cent of the body weight, and in doves 3.5 per cent; hence their metabolism per kilogram, when corrected for skeletal weight, would be increased by amounts corresponding, respectively, to these percentages. The difference in rate between the two species, however, would remain almost as great as before the correction was made. Data for dry skeletal weight, in terms of median percentage of body weight, were obtained for 4 races of pigeons (chapter 11). The adults of the 3 small races (Tippler, Magpie, *SA-E*) had an average body weight of 305 gm. and a relative skeletal weight of 3.9 per cent; Runts have a weight of 560 gm. and a relative skeletal weight of 4.52 per cent. The average basal metabolism per kilogram per hour of the first group (3 races) is 4.21 calories, that of Runts 3.56 calories. The difference (about 17 per cent) in metabolic rate is much too large to be accounted for by the 0.6 per cent difference in amount of dry skeletal material. When the combined contribution of feathers and skeleton—both considered as inert material—is taken into account in calculating the heat production (per unit of body weight), the correction amounts to 12.4 per cent for the 3 smaller races (*M*, *T*, *SA-E*) of pigeons, and 11.3 per cent for the doves as a group.

The dry skeletons of young doves and pigeons (both sexes) were approximately 5 per cent lighter than those of adults; this, however, corresponds to a difference of only 0.2 per cent in the total body weight. The observed sex differences in skeletal weight are not sufficiently consistent to demonstrate an influence on the metabolic rate.

SUMMARY AND CONCLUSIONS

Earlier studies in this laboratory indicate that the anterior pituitary gland produces two hormones which affect (increase) the heat production of pigeons. It seems probable that prolactin acts chiefly on tissues of the intestine, liver, and pancreas, but the extent of its effect on heat production, as this was measured in the present study, is uncertain; since thyroidectomy alone reduces the basal metabolic rate almost as much as does removal of the pituitary, the effect of prolactin probably is not large. Thyrotrophin, through its action upon the thyroids, is a powerful stimulator of heat production in doves and pigeons. Adrenalectomy, in short-term tests, has little or no effect on the heat production of pigeons.

A consideration of heart size in relation to heat production in several types of healthy doves and pigeons leads to the conclusion that no close or consistent association is evident in the present material. There is no significant correlation between heart weight and rate of heat production in pigeons at 20°, nor in ring doves at 30°, 20°, and 15° C. It should be noted that heart size was measured in birds in the nonfasting state, whereas metabolism was measured at the end of a 24-hour fast.

Although the rate of heat production of scraggly pigeons was markedly higher than that of closely related types (ataxic and normal, *SA-E*), the concentration of hemoglobin in the blood was practically identical in the three types. The number of erythrocytes was significantly lower in the scraggly than in the ataxic and normal types.

In the few races in which the weight of the feathers was measured, it varied from 7.1 to 9.2 per cent of the body weight in pigeons, and from 6.95 to 8.75 per cent in doves. These percentages also represent the precise amounts by which the values obtained for metabolic rate of different races would be increased if the feathers were considered as "nonmetabolizing" material (deducted from body weight) in the calculation of their heat production. The relation of varying amounts of plumage in these few types to the rate of heat production at 30°, 20°, and 15°, and to the increase in heat production at 15° over that at 30° C., was studied. The influence exerted upon the metabolism by the plumage, both as inert tissue and as heat-insulating material, is evaluated or discussed.

The plumage of male pigeons is 1.0 per cent, and that of male doves 0.6 per cent, heavier than that of females; correction for these differences in "nonmetabolizing" material would increase the heat production of males relative to that of females by corresponding amounts.

In young pigeons the plumage is 1 per cent lighter, and in young doves 0.5 per cent lighter, than in adults. The metabolic rates as calculated should be reduced, therefore, by 1 per cent in young pigeons and by 0.5 per cent in young doves, when their metabolism is compared with that of the adults.

The effect of excess plumage weight, through restriction of heat loss, was not measured; though this effect may be considerable, it was not the basis for more than a part of the racial differences observed among either ring doves or pigeons.

The effect of the skeleton as "nonmetabolizing" material was evaluated for a few types of doves and pigeons. The dry weight of the skeleton is 0.5 per cent greater in pigeons than in doves, hence the calculated metabolism of pigeons is subject to a 0.5 per cent greater increase than that of doves. The dry weight of the skeleton, referred to body weight, is 0.3 per cent less in young pigeons than in adults, and it is about 0.2 per cent less in young doves than in adults. The differences in skeletal weight between races of doves, and between races of pigeons of similar size, are not large enough to influence appreciably their relative metabolic rates. As between Runt pigeons and the 3 small pigeon races studied, however, the difference in skeletal weight is 0.6 per cent, and if this were recognized in the calculations it would tend to increase the metabolism of Runts to that extent in relation to the other races.

The effect of treating feathers and skeleton collectively as "nonmetabolizing" material in calculating the metabolic rate of adult pigeons and doves per unit of weight would be to increase the actual values about 10 to 13 per cent according to the race; this procedure would have comparatively little effect, however, in equalizing the diverse rates associated with large differences in body size, e.g. between doves and pigeons, or between small and large races of pigeons.

The total amount of dry skeleton and plumage is sufficiently different in young and adult birds to make possible a reduction of the difference in their metabolism of 1.3 per cent for pigeons and 0.5 per cent for doves of different age.

17

THE INFLUENCE OF AGE ON METABOLISM

Introductory and Historical

The study of the basal metabolism of man at different stages of life has received considerable attention. From measurements on large numbers of individuals, standard curves have been constructed showing the average heat production at different ages from early childhood to 60 years or above. These have been supplemented by special studies on infants and children, as well as on elderly persons between 60 and 90 years of age—sometimes by repeating the observations on each subject over a period of years. It has been shown that the basal metabolism, per square meter of body surface, is lowest in the infant at the time of birth; that it rises sharply during the first year of life, and apparently attains a maximum level somewhere between the first and fifth years. From this time onward it declines rather rapidly until the age of 20 or 25, after which it continues to fall throughout adult life at a regular and slow rate; this rate, according to the various standards, lies between 1 and 5 per cent for each 10-year period. Since the effects of age on metabolism may be obscured by growth (increase in size), as in adolescence, it is safer to compare adults of equal weight and height. The uncertainty inherent in the assumption of equality in metabolism according to surface area is thus largely eliminated.

Repeated observations on elderly persons over a period of years have made it possible to compare directly the total heat production at different ages by the same individuals who have not undergone any appreciable changes in weight. As a result of such studies it has been found that there may be a considerable fall in metabolism with age in some subjects, but little or no decrease in others. This method reveals individual differences, and should be valuable in the analysis of the factors which determine senescence. Moreover, it rules out any possible effect of selection, resulting from a dependence of length of life upon intensity of metabolism, which might change the slope of the age curve obtained from group studies.

Du Bois[1] has summarized the work, up to 1936, dealing with metabolism and old age, and concludes "that there is a great deal of variation in old people, probably depending upon the degree of senility, and that if the general slope of the lines of the standards are continued into old age, the Harris Benedict level is somewhat too low and the Aub and Du Bois and Boothby levels a little too high."

In their studies on normal human subjects Boothby, Berkson, and Dunn[2] found that the mean calories per square meter per hour at age 20 was 41.6 for men and 35.5 for women; and at age 60 it was down to 35.7 and 32.8, respectively, a reduction in each sex of about 9.3 per cent. More recently McCay[3] concluded that "the decline of basal metabolism with the weight of years is probable. . . . As the body fails, the basal metabolism decreases with the other powers."

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[1] Du Bois, E. F., Basal metabolism in health and disease, p. 169 (3d ed., Lea & Febiger, Philadelphia, 1936).

[2] Boothby, W. M., J. Berkson, and H. L. Dunn, Amer. Jour. Physiol., 1936, vol. 116, p. 468.

The rat has been used more than any other animal to ascertain the effects of age, and the accompanying complication of increased size, upon metabolism. It has been observed[4,5] that, when measured at low temperature, the heat production per unit of area of small rats was greater than that of large rats; in comparisons made at thermal neutrality (28° to 31°), however, the metabolism was nearly the same in rats of different size.[5,6] In the study of Mitchell and Carman[6] there was found to be no significant difference in the rate of metabolism in rats between the ages of 59 and 188 days, but a definitely higher rate in 30- to 40-day rats as compared with the older group.

In an earlier study by Benedict and MacLeod[7] it was reported that beyond the age of two months there was a steady rise in the basal metabolism with increasing age of female rats studied at 26° and at 29°; the same result was reported for a smaller number of males. These rats, however, were maintained at lower temperatures prior to the time of measurement. Later investigations[8–12] furnished evidence for a decrease in metabolism with increase in size and age in rats. For example, it was found[8] that the average heat production of 12 medium-sized male rats, weighing 307 to 396 gm., was 708 calories per square meter per day; for 12 large but only slightly older male rats (407–562 gm. in weight), 664 calories; and for 2 very large and distinctly older males (723 and 797 gm.), 612 calories. These studies provided information in regard to rate of heat production during early maturity, but gave no clear evidence of the influence of age apart from increase in size. During their second and third years of life determinations[13] were made at 28° upon rats which were previously kept for 24 hours at the same temperature. A nearly constant level of metabolism at different ages was observed for each sex (6 males and 14 females). The authors called attention to the difficulty of evaluating the effect of age on metabolism in growing animals, since rats of diverse size but of similar age had given different results, even when metabolism was calculated per unit of surface. It is, also, their opinion that the rise in metabolism with increasing age observed by Benedict and MacLeod[7] might have resulted from keeping the animals at lower environmental temperatures prior to the determinations. A later report[14] was based on determinations of metabolism in about 100 rats more than 1 year old. The results in their entirety indicated a slight decrease in per capita basal metabolism, associated with small decreases in weight (loss of fat, water?) in most of the animals, and at the same time a slight increase in metabolism per unit of weight or per unit of surface. For groups of rats of similar weight there was a somewhat higher total metabolism in old age than in middle age. Black[15] reported a higher metabolism for 11 rats aged 700 days than for 11 others of equal weight aged 7 to 8 months. In this oldest group of rats, as in those of Benedict and Sherman, there may have been a state of old-age tenseness which did not exist at an age of 8 months or earlier, although the old rats were observed to be quieter than the younger ones. In an attempt to rule out all muscular activity and tonus, Davis[16] recorded measurements made on 136 rats in a dozing condition and in sleep. In each of these states it was found that the rate of metabolism decreased between the ages of 1 and 30 months. The fall was more rapid during the first 4 months, but, whether the rate was calculated per unit weight or per unit surface, it continued steadily throughout adult life.

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[3] Cowdry, E. V., Problems of ageing, p. 680 (2d ed., Williams & Wilkins Co., Baltimore, 1942).

[4] Hill, A. V., and A. M. Hill, Jour. Physiol., 1913, vol. 46, p. 81.

[5] Houssay, B. A., and A. Artundo, C. R. Soc. de biol., 1929, vol. 100, p. 124.

[6] Mitchell, H. H., and G. G. Carman, Amer. Jour. Physiol., 1926, vol. 76, p. 385.

[7] Benedict, F. G., and G. MacLeod, Jour. Nutrition, 1929, vol. 1, p. 367.

[8] Benedict, F. G., K. Horst, and L. B. Mendel, Jour. Nutrition, 1932, vol. 5, p. 581.

[9] Horst, K., L. B. Mendel, and F. G. Benedict, Jour. Nutrition, 1934, vol. 7, p. 251.

[10] *Ibid.*, p. 277.

[11] Sherwood, T. C., Jour. Nutrition, 1936, vol. 12, p. 223.

[12] Swift, R. W., and R. M. Forbes, Jour. Nutrition, 1939, vol. 18, p. 307.

[13] Horst, K., L. B. Mendel, and F. G. Benedict, Jour. Nutrition, 1934, vol. 8, p. 139.

The relatively high metabolism of the "hairless" rat, under nembutal anesthesia, has been reported[17] to show a decrease with age, with accompanying changes in the skin. In 4 adult dogs, maintained under conditions of daily exercise and a high protein diet, Kunde and Nordlund[18] observed no decrease in basal metabolic rate (per unit of surface) over periods of 2 to 12 years. Changes in rate of heat production in the life cycle of domestic fowl[19] were found to follow a course similar to that in man. The metabolism was lowest at the time of hatching; it increased rapidly to a maximum at 30 to 40 days, then decreased to an adult level at 70 to 80 days.

The heat production of Tippler pigeons at different ages was shown[20] to follow a course similar to that in the domestic fowl. Starting at a low level at or shortly after hatching, it rose sharply to attain a maximum at approximately the 10th day, then declined rapidly to an adult level at about the 38th day. Thereafter, in birds studied only to the 421st day, the basal metabolism decreased slightly.

RESULTS OBTAINED ON DOVES AND PIGEONS

A few types of pigeons were measured (409 measurements) between the ages of 2.0 and 4.5 months. The body weights of these young birds were 6 to 13 per cent less than those of the adults with which their rate of heat production will be compared. No measurements were made of young ring doves. Pigeons older than 5 years were classed as "old." At 5 years most pigeons are certainly not old.

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[14] Benedict, F. G., and H. C. Sherman, Jour. Nutrition, 1937, vol. 14, p. 179.

[15] Black, A., Jour. Nutrition, 1939, vol. 17, p. 361.

[16] Davis, J. E., Amer. Jour. Physiol., 1937, vol. 119, p. 28.

[17] Schopback, R. R., C. E. Keeler, and H. A. Greenberg, Growth, 1943, vol. 7, p. 83.

[18] Kunde, M., and M. Nordlund, Amer. Jour. Physiol., 1926, vol. 80, p. 681.

[19] Mitchell, H. H., L. E. Card, and W. T. Haines, Jour. Agric. Res., 1927, vol. 34, p. 945.

[20] Riddle, O., T. C. Nussmann, and F. G. Benedict, Amer. Jour. Physiol., 1932, vol. 101, p. 251.

although that age is nearly 10 times the age they require to reach sexual maturity (see chapter 7). Concerning the longevity of pigeons Levi[21] states: "Long life depends to a great extent, upon the strain. . . . If the pigeon fancier has a hen of any kind which at the end of seven or eight years is still breeding well, she is a splendid hen from which to save offspring. . . . In a good strain of commercial birds, the hens should breed very satisfactorily for five years." A few records indicate that pigeons have attained or exceeded the age of 20 years. The average age of the pigeons classed as old in the present tests was 78.5 months. Relatively large groups of doves were measured at ages in excess of 55 months, and such birds are here classified as "old" doves. Ring doves aged no more than 55 months are not old, in fact, since 6 doves (all males) in our own colony have attained to ages between 103 and 167 months. At 55 months, however, doves are usually beyond the prime of life; and in order to have a sufficient number of "old" individuals in these tests, the lower limit was set at that age. The average age of this group of doves was 71.7 months.

TABLE 66

Comparison of heat production (calories per kilogram per hour) in certain types of young pigeons (aged 2.0 to 4.5 months) with data obtained from adults (4.5 to 60 months) measured at the same season and temperature. The number of birds measured is given in parentheses.

Kind of pigeon	Sex	30°				20°			
		Adult	Young			Adult	Young		
		Calories	Calories	Number	Per cent change (+ or −)	Calories	Calories	Number	Per cent change (+ or −)
Tippler.	♂	4.06	5.06	(9)	+24.6	4.34	5.05	(86)	+16.3
Tippler.	♀	4.39	4.82	(16)	+ 9.8	4.56	5.22	(62)	+14.4
Carneau.	♂ ♀	3.64	4.21	(184)	+15.7	4.02	4.54	(28)	+12.9
Scraggly (SA-R)	♂ ♀	4.90	6.30	(3)	+28.4	6.99	7.24	(5)	+ 3.6
Other types. . . .	♂ ♀	3.78	4.56	(9)	+20.6	4.54	4.87	(7)	+ 7.3

The relation of rate of heat production in young pigeons to that in adults is shown by the complete data provided in various tables (45–64), and in summarized form in table 66. The summary indicates that in measurements made at 30° the metabolic rate of groups of young exceeds that of corresponding adult groups by percentages which range from 9.8 to 24.6 (perhaps 28.4) per cent. At 20° the values obtained from the young exceed those for adults by smaller percentages, ranging from 3.6 to 16.3.

It must be noted, however, that all the percentages just named are subject to reductions which can be evaluated only in part. The young birds were slightly smaller (6 to 13 per cent) than the adults, and the differences listed in the table relate to calories per kilogram per hour. If surface were properly considered, the values for heat production of the young (smaller) birds would be slightly reduced. Again, in young pigeons the feather weight (nonmetabolizing tissue) is less, by approximately 1.0 per cent of the body weight, than it is in adults (see chapter 11). For this reason alone all the percentages listed above are subject to a reduction of 1.0 per cent. Moreover, a smaller relative amount of this heat-insulating material seems to be regularly associated with a higher rate of heat production (see chapter 16). This effect, though it was not measured, could account for a considerable fraction of the differences observed (table 66); and it seems probable that the large differences observed at 30° reflect the influence of this factor more than do the smaller differences observed at 20°. Apparently, therefore, the rate of heat production of young pigeons is at least 8 to 12 per cent higher than that of adults, but there is a question as to the extent to which this residual difference depends on an extrinsic factor—a smaller amount of heat-insulating material in the young pigeons.

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[21] Levi, W. M., The pigeon (R. L. Bryan Co., Columbia, S. C., 1941).

Complete data for heat production in "old" doves and pigeons are given in various tables (14–64) and a summary is provided in table 67. The data obtained for doves will be considered first. Since very unequal numbers of "old" birds of the different races or hybrid types were tested, it seemed advisable to calculate in two ways the "per cent change" observed in each large group or class of birds. This was first done by giving all races (types) equal rank in the tabulation of "per cent change" with age, despite the variation in number of individuals within these types; thereafter, a second average was calculated in the usual manner (table 67). The two types of calculations yielded values which, for most of the ten sets of determinations, are in very fair agreement. It seems, therefore, that the use of large numbers of old birds of some races and very few of other races did not materially affect the results. At 30° the rate of heat production in older birds is found to be 3 to 4 per cent less than that in adults. At 20° a similar difference was not found: for the main group of (149) females the value obtained for the older birds (−0.4 per cent) represents equality, or a negligible difference; for the main group of (185) males the older birds show a slightly higher metabolic rate (+1.6 per cent) than the adults with which they are compared. Certainly the latter value, like practically all the 20° values, is significantly different from the value (−3.5 per cent) obtained from (136) males at 30°. At 15° the metabolic rate of the older males was again equal to that of the adults, whereas older females apparently had a slightly lower rate (−3.3 per cent) than adult female doves.

The rate of heat production in older pigeons showed a rather marked reduction—a definitely greater reduction than was observed in older doves. Measurements made on two groups at 30° gave average reductions of −11.9 and −7.3 per cent. At 20° the average metabolic rates for older birds were lower than those for adults, but by only 4.4 and 4.7 per cent. Additional tests on older pigeons, on females particularly, would have been desirable, but the conclusions stated above seem to be warranted by the 221 measurements made on older pigeons.

TABLE 67

COMPARISON OF HEAT PRODUCTION (CALORIES PER KILOGRAM PER HOUR) IN RELATIVELY OLD DOVES (55+ MONTHS) AND PIGEONS (60+ MONTHS) WITH DATA OBTAINED FROM ADULTS (4.5 TO 55 OR 60 MONTHS) MEASURED AT THE SAME SEASON AND TEMPERATURE. THE NUMBER OF MEASUREMENTS (OR OF TYPES MEASURED) MADE ON THESE OLDER BIRDS IS GIVEN IN PARENTHESES.

AVERAGES CALCULATED FOR TYPES OR INDIVIDUALS MEASURED	SEX	30°				20°				15°			
		ADULT	OLD			ADULT	OLD			ADULT	OLD		
		Calories	Calories	Number	Per cent change (+ or −)	Calories	Calories	Number	Per cent change (+ or −)	Calories	Calories	Number	Per cent change (+ or −)
Dove types	♂	4.54	4.35	(18)	−4.2	6.19	6.31	(19)	+1.9	7.24	7.22	(16)*	−0.3
individuals	♂	....	....	(136)	−3.5	....	....	(185)	+1.6	....	....	(34)	+0.3
Dove types*	♂	4.53	4.38	(7)	−3.3	6.18	6.35	(6)	+2.8	....	....	....	.....
individuals*	♂	....	....	(17)	−2.3	....	....	(11)	−1.3	....	....	....	.....
Dove types	♀	4.87	4.66	(13)	−4.3	6.34	6.25	(17)	−1.4	7.25	7.06	(11)*	−2.6
individuals	♀	....	....	(108)	−4.3	....	....	(149)	−0.4	....	....	(21)	−3.3
Dove types*	♀	4.77	4.69	(8)	−1.7	6.19	6.13	(5)	−1.0	....	....	....	.....
individuals*	♀	....	....	(15)	−1.6	....	....	(10)	−3.4	....	....	....	.....
Pigeon types	♂	4.02	3.58	(7)	−11.0	4.44	4.35	(7)†	−2.0	4.70	4.76	(2)	−1.3
individuals	♂	....	....	(58)	−11.9	....	....	(93)	−4.4	....	....	(5)	+6.8
Pigeon types*	♂	4.06	3.93	(8)‡	−3.2	....	....	....	.....	....	....	....	.....
individuals*	♂	....	....	(28)	−7.3	....	....	....	.....	....	....	....	.....
Pigeon types*	♂ ♀	....	....	....	.....	4.21	3.96	(11)§	−6.0	....	....	....	.....
individuals	♂ ♀	....	....	....	.....	....	....	(37)	−4.7	....	....	....	.....

*Types measured at only one or two seasons, not at three or four seasons as were the types listed above.

†One group (of 7) females included in these tests.

‡One female only included in these groups.

§Only 3 groups (5 individuals) of females in these tests.

Discussion

It is necessary to consider the question whether the observed reductions in metabolic rate during aging in doves and pigeons are traceable to extrinsic (or similar) sources. On this point it can be said that, in both species, the changes in body weight were slight; in doves no appreciable change occurred; in most, but not all, races of pigeons there was a tendency for the body weights of older birds to exceed the adult weights of the same birds by a few to several grams. Though body fat is usually present in only small amounts in both doves and pigeons, it would perhaps be expected to increase somewhat in old birds. Whether body fat did, in fact, increase in these birds is not known; but the inspections and notes made on all autopsies leave no doubt that if such increases occurred they did not result in marked accumulations of visible fat.

In view of the importance of plumage weight as an extrinsic regulator of heat radiation, some additional data for plumage weight in old birds would have been useful. The known laws of feather growth would preclude any increase in the number of feathers, and a decrease in feather number is highly improbable, but feather weight and texture are probably subject to modification in old age. Feather weight was measured in only a single old bird. This was a purchased female Magpie whose age was at least 6.5 years. The plumage weight of this bird was both absolutely and relatively less than that of the 2 adult female (also of 2 male) Magpies, and relatively (not absolutely) less than that of 2 young female Magpies which were also measured. Indeed, in this bird the plumage weight was relatively the lightest found in any of the 65 pigeons whose plumage weights were determined. The available evidence suggests, therefore, that old pigeons have less heat-insulating material than is present in younger adults; and this deficit would probably tend to maintain the heat production of old birds nearer to the adult level than would otherwise be the case.

Evidence on the role of extrinsic factors in these birds may be summarized as follows: A slight increase in body weight, and a possible slight accumulation of fat, would both tend (when properly included in calculations) to increase the rate of heat production in old birds as this is presented in tables 66 and 67. On the other hand, it is probable that these tabulated values were attained with the aid of relatively deficient heat insulation, which provided a higher degree of stimulation than was present in the adults. These considerations indicate the complexity of the problem, but they do not seem to invalidate the conclusion that measurements made at 30°, particularly in pigeons, indicate that the aging process was accompanied by a measurable reduction of the metabolic rate. It should be noted, however, that the rate at which heat production decreases with age in pigeons is much less than the value once used by us[22] to correct for the age factor. The age here called old probably corresponds better to late middle life.

As for intrinsic factors which may be associated with the observed changes in metabolic rate in old age, there is, specifically for doves and pigeons, only the fact that their thyroids tend to increase in size with advanced age.[23] Payne[24] has shown that in fowl the effects of aging are particularly marked in the anterior pituitary glands. In cocks aged 9 to 13 years a loss of function in basophilic cells, and reduced activity in acidophilic cells, was reported. Obviously, however, any organic changes which would establish chronic undernutrition in some old birds would tend to reduce the average heat-production values obtained from groups of old birds. Whether such conditions arise in doves and pigeons, and the extent to which they may occur, seems to be quite unknown.

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[22] Riddle, O., G. Christman, and F. G. Benedict, Amer. Jour. Physiol., 1930, vol. 95, p. 111.

Conclusions

In terms of calories per kilogram of body weight, the rate of heat production in young pigeons, aged 2 to 4.5 months, was found to be measurably greater than that in adults aged 4.5 to 60 months. A total of 409 measurements were made on young birds; the values obtained for young birds are compared with results obtained at the same season for much larger numbers of adult pigeons. At 30° the heat production of young birds exceeded that of adults by 15 to 20 per cent. At 20° this excess in young birds was 12 to 15 per cent. These values are 1.0 per cent too high because of lower weight of plumage in young birds, and slightly too high because the body weights of the young birds were 6 to 13 per cent less than those of adults.

The extent to which heat production in the young was stimulated by the extrinsic factor, possession of less heat-insulating plumage, cannot be evaluated.

From 686 determinations made on doves of advanced age (average 71.7 months; called "old"), the heat production at 30° was found to be 3 to 4 per cent lower than that of adults aged 4.5 to 55 months. At 20° the results obtained were different. The most reliable group of measurements indicated that heat production was practically the same (−0.4 per cent in the old) in old and in adult females; the heat production in old male birds exceeded that found in adults by approximately 1 per cent.

A total of 221 determinations made on pigeons of advanced age (average 78.5 months; called "old") indicated that the heat production of these birds at 30° was 7 to 12 per cent less than that of adults aged 4.5 to 60 months. At 20° the old birds produced only 4 to 5 per cent less heat than the adults.

The percentages of change associated with old age are subject to three slight corrections: (*a*) In some, though not in all, races a slight increase in body weight occurred in the older birds; (*b*) a slight increase in body fat may have occurred in the older birds; (*c*) meager evidence indicates that in pigeons the plumage weight becomes relatively less with age. If these items were made a part of the calculations they would tend to increase slightly the rate of heat production in older birds relative to the values recorded for adults. On the other hand, an indirect but more important effect of less adequate plumage in old birds—if such inadequacy exists—would develop as a consequence of the smaller amount of heat insulating material. This would probably provide a greater stimulus to heat production in the older birds than was present in the adults.

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[23] Riddle, O., and W. S. Fisher, Amer. Jour. Physiol., 1925, vol. 72, p. 464.

[24] Payne, F., Biol. Bull., 1942, vol. 82, p. 79.

The only intrinsic factor which has been associated directly with the aging processes in these doves and pigeons is a tendency for their thyroids to enlarge. Other factors probably exist.

18

CONCLUDING STATEMENT

Most of the results of the present study have been summarized at the ends of preceding chapters, and those results will not be reviewed here. The present statement is mainly concerned with the association, or combination, of traits in the various racial types of doves. Dove races and hybrids, rather than pigeons, are here of chief interest, since they were established by our own selection and breeding procedures. As an aid to comprehension of the marked biological inequality of these dove races, it seemed necessary to construct a table in which the several outstanding racial characteristics, as these were measured in this study, can be more readily observed and compared.

In table 68 the more important races and hybrids are listed in the order of their body weight (smallest types at top). An adjacent column is used to designate, in a suitable manner, that body weight was quite low[1] or quite high in certain races and types. Subsequent columns supply similar records for extreme expressions of eleven different traits. The plus (+) and minus (−) signs used for this purpose are self-explanatory. The term "extreme" applies to values at or quite near to the maximum or minimum observed in the 40 types of doves listed. Blank spaces in columns usually mean that "intermediate" values were obtained. In some cases, however, the blank spaces mean that no measurement of a particular trait was made. Doubt concerning any particular case can be resolved by consulting the complete data in the appropriate chapter. Two traits (response to prolactin; anterior pituitary weight) were measured in relatively few types, and in these cases the absence of data is indicated by a zero (0). This same symbol is used to indicate those types whose heat production was not measured, or for which the number of measurements was inadequate. Several types which disappeared early were not studied for "heart weight," since weights of that organ were not taken during the first six years of this study. Those races and hybrids which were studied least adequately are not included in this tabulation. It will be recalled that the various organ weights (e.g., liver weight, egg weight, etc.) were meas-

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[1] The smallest dove race (*NA*) was extreme with respect to five additional traits, and all these represented the low (−) extreme. Since *Streptopelia douraca* represented one-eighth of the ancestry of this race (races 206 and 29 contained still higher fractions of *douraca* blood, but both of those races were lost early), and since that pure species was observed by us to mature later than is usual in *St. risoria*, "least early" maturity in race *NA* may have been influenced by *douraca* ancestry. Whether other extreme traits of this race were similarly derived, or whether they have a more intimate relation with extremely low body weight in doves, is unknown. Race *NA* was the only race having dark color (this was derived from *St. douraca*); elsewhere dark color was present only in a fraction of *NA* × 72 hybrids.

TABLE 68

Characteristics associated with important races and hybrids of ring doves. Extreme states are designated plus (+) or minus (–). Zero (0) indicates that the trait was not measured.

Race or hybrid	Body weight		Thyroid wt.	Liver wt.	Intestinal lgth.	Response to prolactin	Anterior pituitary wt.	Early maturity	Testis wt.	Egg wt.	Heart wt.	Heat production
	Actual	Sex difference										
NA	–	–		–		–	0	–			–	
6	–			+	+	0						0
51	–	–	–			–	–	–			+	+
75	–		–	+			+			+	+	+
63				+			0	+	+	+	–	
44		–	–	+	+	0	0	+	–	–		0
36				–		0	0		–	–		–
W						–	0					+
N2		–			+	+		–		–	–	+
B		+	+	–	–	–	+			+		
OT					–	0	–					–
72		+	+		–		+	–				
62		+	+		+		–			–		–
NE	+	+	–			0	0		–	+		0
65	+					–	0	–				
67	+	+			–	0	0		+			–
78	+			–	–	0	0	+	+			0
NE × N2	–	–				0	0					+
75 × B	–	+				0		+	–			
N2 × 44	–			+	+	0						+
51 × 63	–	+	–			–	0					
63 × N2		–			+	0	0		–		–	
51 × 44			–			0	0					0
11 × 62			+	+		0	0	+			–	
N2 × OT					+	0	0		+			0
63 × 62				–			0	+			–	–
36 × 62		+		–		0	–			–		
NA × 72		+		–	–	–		–			+	
36 × B				+		0	0		–			
36 × 72				+		0	0		–	+		
63 × 72										+		
72 × 75		–				0	0					+
72 × OT					–	–	0	–				–
63 × 44					–	+	0					
61 × 63			–			0	0					0
B × 62			+			+	0				+	
67 × 72	+					0	0	–	+			–
72 × 62	+		+	–	–	0	+			–		–
62 × 75	+					–	0		+			
N2 × 62	+	–			+	+	0					

ured as "percentage of body weight"; for convenience that phrase is omitted in the column headings of table 68.

The fact that a sex difference in body weight (males heavier than females) was established in some of these races and not in others is of much interest. It was not consciously selected for, but was a by-product of other selection. Again, it might be expected that the measurements of several traits in the various races, as these are presented in table 68, would throw light on endocrine factors associated with sex difference. That expectation, however, is fulfilled only in small measure. It is found that two of the races, and also two hybrid types, which showed *least* sex difference were among the very few (seven) types having extremely *high* rates of heat production (probably therefore with high thyroid function); and two races showing *greatest* sex difference were among the seven types having extremely *low* metabolic rates. No contraindication of this type of relation is supplied by these data. In the races, but not in the hybrids, there is perhaps slight evidence that extremes of sex difference may be related to the age at which sexual maturity was attained. Three of the four races which showed least sex difference in body weight were late-maturing races, and one race (*72*) and one hybrid (*NA* × *72*) which showed most sex difference in body weight were late-maturing types; in only one case (race *44*) was minimum sex difference in weight associated with early sexual maturity. Thus, in four of five types, one or the other extreme of sex difference in body weight was associated with late sexual maturity. In one race (*67*) maximum sex difference in body weight was associated with extremely small testes; in race *NE*, however, an opposite relation was found, and the present data fail to indicate that relative size of testes is associated with body-weight differences in the sexes. This, of course, does not directly bear on the question of the effect of androgens (and interstitial testis) on the body weight, since it is not known whether hormone production is proportional to testis weight.

The three hybrid types (*72* × *62*, *B* × *62*, and *11* × *62*) which had extremely large thyroids were derived wholly from races with extremely large thyroids. On the other hand, the three hybrid types (*51* × *63*, *61* × *63*, and *51* × *44*) which had extremely small thyroids were derived from parents (one or both) with extremely small thyroids. Small thyroids are twice associated with large size of liver, and twice large thyroids are associated with extremely small livers; in only one case (*11* × *62*) were both thyroid and liver extremely large, and in no case were both of these organs extremely small. "Plus" thyroids are associated with "minus" intestinal length in three cases, and the reverse is found in one case; in one case both organs are of "plus" type. In four cases "minus" values for liver weight and intestinal length were associated, and there are three cases of associated "plus" values; in no case was a "plus" for the one of these organs combined with a "minus" value in the same racial type. There is thus evidence that, as racial traits, liver and intestine tend to vary in the same direction; and, in these dove types, that direction is usually opposite to that observed for thyroid weight, although it may parallel thyroid activity. Important evidence on this latter point is found in the fact that in two races "minus" thyroids were associated with "plus" heat production, and in two other races "plus" thyroids were associated with "minus" heat production. No association of the opposite type was observed.

Thyroid size can here be seen to bear no constant or significant relation to response of the crop sacs to prolactin. Large thyroids were associated with large anterior pituitary glands in three racial types; in one race the thyroids were small and the pituitary large; in a fifth case the reverse was found. These results indicate that, although the pituitary controls thyroid function, the pituitary weights obtained by us did not provide information concerning levels of thyroid function.

It was noted above that, for the races and types listed in table 68, extreme values for liver weight and intestinal length tend to vary in the same direction, but usually (not always) in the opposite direction to that of thyroid size. The relation between liver weight on the one hand, and thyroid weight and heat production on the other, was not satisfactorily determined by the data obtained in this study. The meager data suggest that small livers are associated with low response to prolactin (races *NA*, *B*, and *NA* × *72*), and that extreme liver size is associated in no constant way with anterior pituitary weight. In all of three types (*63*, *44*, and *11* × *62*) large liver size was associated with early sexual maturity of females, and in one type (*NA* × *72*) small liver size was joined with late sexual maturity. There was no contraindication of this relation. On the other hand, three large-livered types (*44*, *36* × *B*, and *36* × *72*) had extremely small testes, and in one race (*63*) large liver was associated with large testes; in still another race (*36*) small liver and small testes were associated. Three types (*75*, *63*, and *36* × *72*) with large livers laid extremely large eggs, and three types (*36*, *36* × *62*, and *72* × *62*) with small livers laid extremely small eggs. One race (*B*) with small livers, however, produced large eggs.

Associations of intestinal length with traits not mentioned above are worthy of note. It will be observed that in three races (*44*, *N2*, and *62*) very long intestine was associated with extremely small eggs, and in one race (*B*) very short intestine was associated with large eggs. In one hybrid type, however, short intestine was associated with small size of eggs. In three types (*B*, *NA* × *72*, and *72* × *OT*) very short intestines and extremely low response to prolactin are associated, and in two types (*N2* and *N2* × *62*) very long intestines and very high response to prolactin are associated. Since this relation is not contraindicated by any case, it seems probable that relative responsiveness of crop sacs to prolactin is at least one factor in the determination of intestinal length in these dove races. This result is the more remarkable because three types (*B*, *72*, and *72* × *62*) show an association of extremely short intestines with heavy pituitaries; and because relatively heavier pituitaries and longer intestines were associated in the females of nearly all of the few races for which pituitary weight was determined.

Already noted are the data which indicate that those races which gave a high response to prolactin also had large livers and long intestines, and *vice versa*. The lack of evident association of other traits with response to prolactin is possibly a consequence of the small number of types in which the response to prolactin was measured.

Extreme racial traits associated with extremes of heat production have been partly noted in the paragraphs above. A tendency of small (more efficient?) thyroids to be associated with a high metabolic rate, and perhaps of large thyroids to be associated with low metabolic rate, was noted. Two factors tend to make the associations with thyroid weight less regular than would otherwise be found. First, large size of thyroids may indicate either under- or overproduction of thyroid hormone; also, during most of the period covered by this study some endemic goiter was certainly present in most dove races. Second, the method used in calculating the heat production of these races apparently results in a slight tendency to assign higher than true values to small races, and lower than true values to larger races. Although differences in body weight are not large, they involve a difference in body surface which was not properly equalized by the formula ($S = 10 \times W^{\frac{2}{3}}$) used for calculating rate of heat production. The data of table 68 nevertheless clearly show that neither the body weight nor the true surface area was the factor which determined the differences in rate of heat production in most of these racial and hybrid types.

The number and variety of combinations of accentuated traits in these inbred types is an impressive fact which is made evident in table 68. Some of these traits (e.g., weight of liver, testes, and eggs) seem, from the term used to describe them, to be of anatomical rather than of physiological nature. Though this is partly true, it is also true that most of these visceral organs are intimate parts of the endocrine system, and—in comparison with traits such as stature or conformation of the head—have functional significance. It is, therefore, of some importance to note that actual experience has shown that races which possessed some of these combinations of traits could be maintained, whereas other races were difficult or impossible to maintain, under the conditions which prevailed in our colony. Of course, it is wholly probable that other unmeasured traits were usually more important to survival than the ones measured by us. Taking into account the fact that our own incidental procedures (other than inbreeding) contributed to the extinction of some races, it can be said that such combinations of traits as were represented in races *51*, *75*, *63*, *N2*, *72*, and *OT* gave evidence of ability to survive, and to withstand further inbreeding. On the other hand, races *36*, *44*, *NE*, and *78* (also *11* and *29*) gave evidence of inability to survive under the conditions which prevailed in our colony. These considerations support the view that in these doves it was possible to segregate physiological traits which, under inbreeding, were adverse to survival under conditions which permitted survival in races provided with a different set of constitutional factors. The evidence indicates that biological inequality determined chance of survival in these races.

With the exception of small size of testes, which may possibly (not probably) rest on some generalized condition (infection, etc.) that is adverse to optimal health, and of heart weights, for which the observed racial differences were not large, the present data show that extreme expressions of the several traits had a genetic and not an environmental basis. From a population of ring doves, races with and without a sex difference in body weight were segregated, and races with large and small thyroids were formed and maintained. Similarly, from the same population, there were formed (and sometimes maintained) races with long and short intestines, races with extremely high and low response to prolactin, races with larger and smaller anterior pituitary glands (maintenance not proved here), races showing early and late sexual maturity in females, races whose eggs were larger and smaller, and races whose rate of heat production was high in some cases and low in others. The transmissibility of most of these traits in outcrosses was demonstrated.

Whether the segregated groups should be called "races," "breeds," "stocks," or "types" is immaterial. It is wholly probable that numerous humans carry and transmit genetic factors predisposing to each of the extremes of each of the several traits listed above. And the strong presumptive evidence that similar segregates are (theoretically) obtainable within *Homo sapiens* is not contradicted by any valid evidence of which the writer is aware. Moreover, it should be noted that the data hitherto used by anthropologists for the classification of "races" of modern man are predominantly anatomical;[2] either the physiological differences of these races of man (occasionally reviewed in earlier chapters) are little known, or technical difficulties have thus far prevented decisions on the relative roles of heredity and environment. The results of the present investigation thus provide direct experimental support for the view, now prevalent among anthropologists, that the products of endocrine glands do much to shape the anatomical variants with which their measurements deal. These results also lend support to those few anthropologists who conclude that it is not alone "underprivilege which makes the underdog."[3] Widespread genetic inequalities of individuals and groups characterized the organisms here subjected to tests.

Earlier studies conducted in many laboratories have shown that essentially similar laws of inheritance, and quite comparable types of endocrine action, exist in bird and man. It is therefore wholly probable that the endocrine glands bear a similar relation to structures and functions in man and pigeon. In both cases it is known that in part the glands act as controllers of the development of the body and mind. The results of the present research thus provide a kind of evidence, hitherto largely lacking, for the genetic and biological inequality of human individuals, types, and races. Measurements made here, however, are expressed in physiological terms, not in terms of superiority or inferiority. These results nevertheless seem to be applicable to man, and to have important implications for the social sciences and for educational programs. Some of the institutions developed by man, and some of man's philosophy of life, should be affected by the existing evidence that all men are created biologically unequal.

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[2] A recent and impressive exception should be noted: Sheldon, W. H., and S. S. Stevens, The varieties of temperament, a psychology of constitutional differences (Harper & Bros., New York and London, 1942). This study deals mainly with behavioral dynamics and with the interrelations between the static and dynamic levels of personality.

[3] Hooton, E. A., Twilight of man (G. P. Putnam's Sons, New York, 1939).

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